COLOUR PATTERNS OF THE DWARF MINKE WHALE *BALAENOPTERA ACUTOROSTRATA* SENSU LATO: DESCRIPTION, CLADISTIC ANALYSIS AND TAXONOMIC IMPLICATIONS

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Colour patterns of the dwarf minke whale, the most complex of any baleen whale, are described and illustrated. While variability is sufficient to allow recognition of individual whales, distinct colour elements consistently occur, including a light grey rostral saddle, dark grey spinal field and ivory white ventral field. Three dark lateral fields (nape field, continuing ventrally as a throat patch; thorax field; peduncle field) alternate with light grey thorax and flank patches and ivory white peduncle and shoulder blazes, the last variably in-filled by a dark axillary patch. The flipper has a diagnostic white basal blaze and dark grey distal patch. White mandible and eye blazes occur primarily on the right side.

Cladistic analyses were run using 13 colour characters and 12 taxa (11 baleen whales, representing all families; outgroup: sperm whale *Physeter*). The relationships between baleen whale families were poorly reflected in the analysis and no monophyletic groups were extracted. However the analysis suggested that the common minke whale *Balaenoptera acutorostrata* and the dwarf minke whale are most closely related. The common minke , dwarf minke and Antarctic minke whale *Balaenoptera bonaerensis* were also united, as only those species shared a double caudal chevron and discrete light grey lateral patches (anterior thorax and posterior flank patch) separated by a dark thorax field. Light grey lateral pigment, blowhole streaks, ear stripes and a tendency for colour asymmetry characterised most species of *Balaenoptera*. Colour pattern and other available data support Rice's (1998) recognition of the dwarf minke whale as an as yet un-named subspecies of *Balaenoptera acutorostrata*. □ *Cetacea, Balaenopteridae, colouration, phylogeny, taxonomy.*

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Until quite recently, the minke whale was considered to be a single species with one of the most extensive cetacean distributions (Stewart & Leatherwood, 1985). Rice (1998) summarized the morphological, osteological and genetic data and suggested that two species be recognised: the 'common' minke whale *Balaenoptera acutorostrata* (Lacépède, 1804) and the 'Antarctic' minke whale *Balaenoptera bonaerensis* Burmeister, 1867. A review by the Scientific Committee of the International Whaling Commission (IWC, 2001) accepted the recognition of these two species, but deferred a decision on other nominal taxa, including a diminutive or dwarf form (Best, 1985; Arnold et al., 1987; Zerbini et al., 1996) found throughout the Southern Hemisphere, pending a world-wide review of morphological and molecular data.

As part of this general re-evaluation, we present data on colour patterns of the dwarf minke whale, based primarily on field observations. Best (1985) noted several diagnostic features: a dark throat patch, 'Type 3' flipper with dark tip and white base, and a white shoulder patch. He discussed several other colour features in comparison with the Antarctic minke whale. Based primarily on presence of a dark throat patch or Type 3 flipper, he also documented the diminutive form from eastern Australia, New Zealand and Brazil.

External characters, such as colouration, are amenable to field studies and, as with birds, field observations can provide data based on a relatively large sample size (Corbet, 1997). We have recognised over 200 dwarf minke whales on the northern Great Barrier Reef during 1999-2001. We have detailed field colour notes for about 100 individuals in each of 1999 and 2000. We also review photographs from Australia, the South Pacific, New Zealand and Brazil.

With this new information on the colour pattern variation in dwarf minke whales, we compare colour patterns in Antarctic minke whales (Best, 1985; Bushuev & Ivashin, 1986), common minke whales and other mysticetes. We attempt to establish which colour patterns are homologous and establish a consistent terminology for the features. This allows a better documentation of colour pattern details, which are used to recognise individual whales in photo- and/or video-ID studies, as well as discussion of features of possible phylogenetic significance. Colour patterns have been used to assess taxonomic and/or phylogenetic relationships in odontocetes (Mitchell, 1970; Perrin, 1997) but we know of no similar attempts for mysticetes.

MATERIALS AND METHODS

Dwarf minke whales were observed primarily from the dive vessel *Undersea Explorer* as part of a wider study, conducted since 1996, on the biology and behaviour of the whales and management of swimmer-whale interactions during commercial swim-with-whale activities (Birtles et al., 2002; Valentine et al., 2004). Observations of colour pattern were made both from the surface and underwater but rely primarily on the latter, representing over 200 individuals in 1999-2001. Colour patterns, as well as scar patterns, have been used to recognise individual whales. The photo- and video-IDs are being used to document within-season and between year re-sightings (Birtles et al., 2002), which in turn provide information on spatial and temporal distributions of the whales, site fidelity, association patterns and potential for cumulative impacts.

The greatest resolution is obtained from still images; such images, primarily from the field seasons 1999-2002, are used for the illustrations in this paper. Underwater video was routinely used for identification of individuals by colour and scar patterns; it also provided documentation of colour pattern variations. Video was an especially effective tool because (1) it documented animals from different angles so that we could confirm that a lighter feature was actually a colour pattern rather than a reflection of light; (2) it provided clear indications of whether the animal was observed from the right or left sides, and (3) a sequence could contain views of both right and left sides of an individual, allowing matching of the asymmetrical colour patterns. Still images could be extracted from digital video using "DVD Tools". Underwater field colour notes (mainly by RAB) could also be used to assess colour patterns of individuals and could be matched to particular video sequences.

Published and unpublished photographs and video submitted by divers, commercial photographers and scientific colleagues were also examined. These represent an additional 15 animals from Queensland (Arnold et al., 1987: 10; Paterson, 1994: 1; unpublished Queensland Museum records: 4); one from Marion Reef, Coral Sea (Rockman, 1986 a, b); two from New South Wales (Arnold et al., 1987: 1; Australian Museum archives: 1); two from Victoria (Arnold et al., 1987), one from New Caledonia (Laboute & Magnier, 1979), one from Vanuatu (video), 3 from New Zealand (Baker, 1983: 1; unpublished from S. Gibney: 2), one from Fiji (email images from C. Holloway) and 3 from Brazil (Secchi et al., 2003:1; 2 unpublished, from A. Zerbini).

Although it is possible to reverse images on video, this is usually done only by commercial producers who have the appropriate editing facilities. Videos showing a particular side of an animal could therefore be accepted as valid documentation. More care is needed with photographs. We have found transparencies mounted inaccurately but such cases can be checked easily. More problems occur when working from copies of original transparencies, when such checks on the film may not resolve any ambiguity in orientation of the whale. In such cases, we have used a combination of features such as the orientation of the blowhole streaks, posterior extension and shape of the rostral saddle, and extent of white blazes on the mandible and around the eye (see below). Direct observations and analysis of unedited video have shown that such features are consistently asymmetrical and can be used to determine which side the photograph shows.

This paper depends on photographs to document variation in particular features. For the dwarf minke whale, we include a number of previously unpublished images. Adobe Photoshop was used to remove the background from the underwater photographs and to match

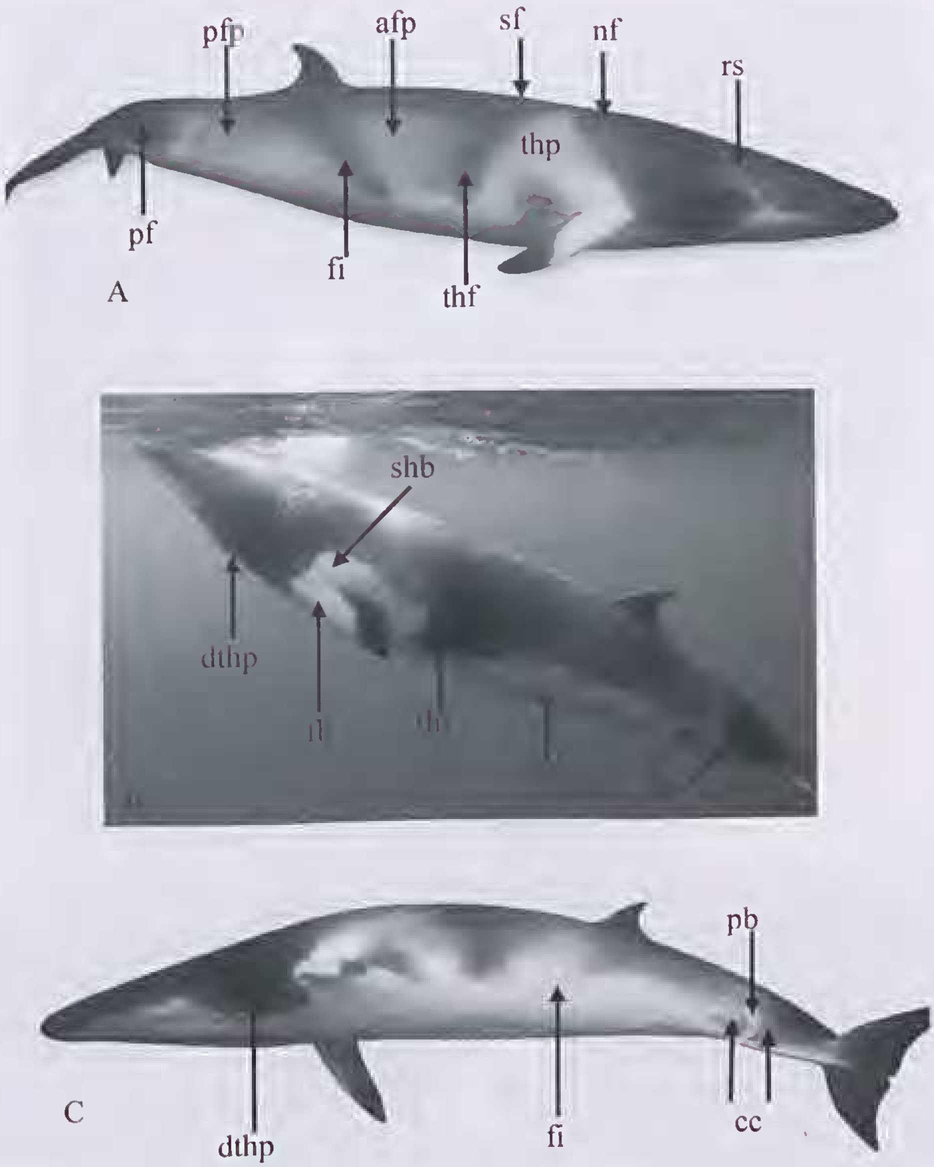
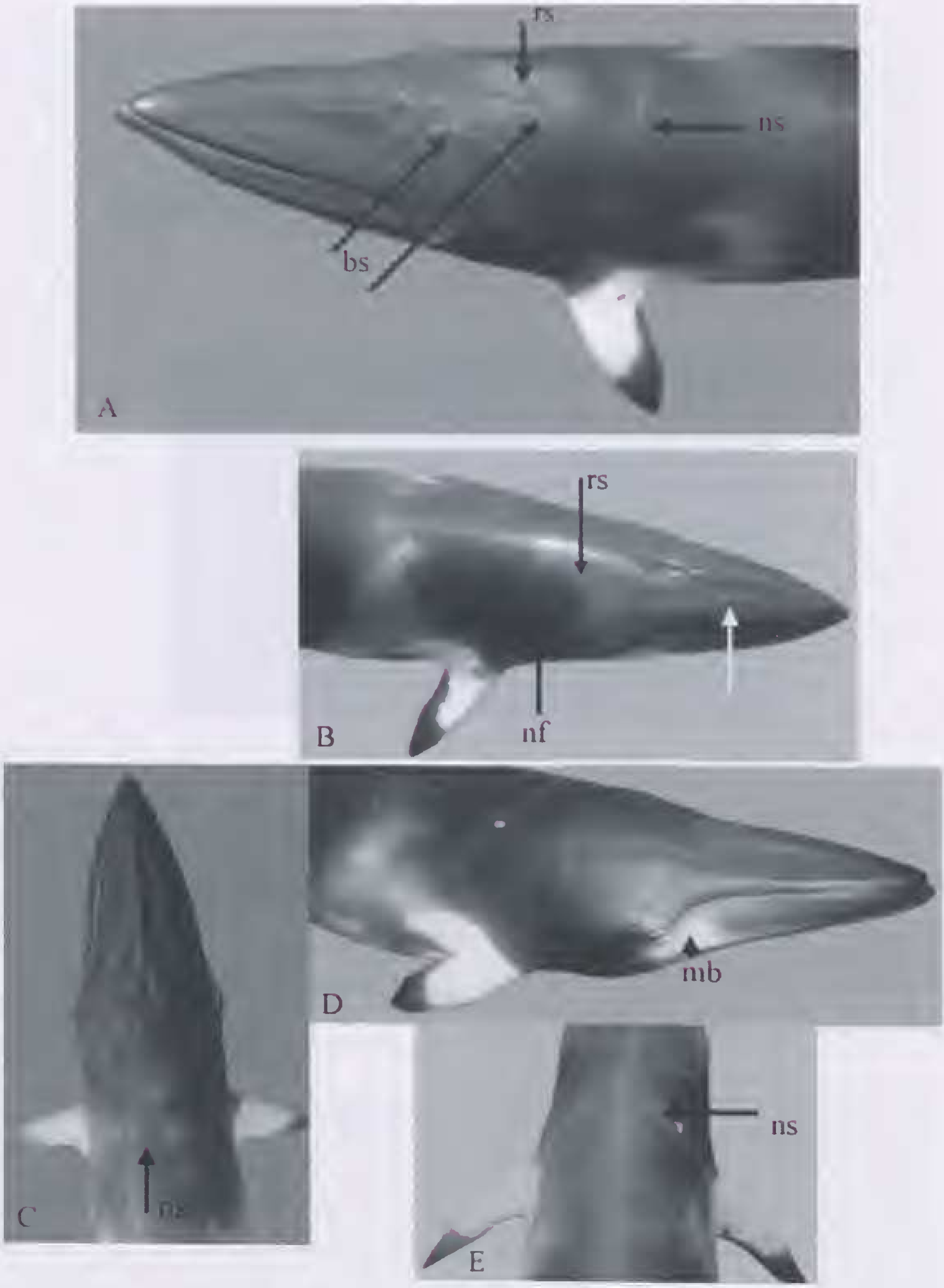


FIG. 1. Colour elements of the dwarf minke whale. A, Right lateral view, showing light rostral saddle (rs) and dark grey spinal field (sf) along the back; overall dark nape field (nf), thorax field (thf) and peduncle field (pf), with alternating light grey thorax patch (thp) anteriorly and flank patch posteriorly, the latter divided by a dark flank infill (fi) into an anterior flank patch (afp) and posterior flank patch (pfp). B, Left lateral view showing white ventral field (vf): dark throat patch (dthp), an extension of the nape field; dark thorax field (thf); double caudal chevron (cc); ivory white basal flipper blaze (fb) and shoulder blaze (shb). C, Ventro-lateral view showing ivory white ventral field; dark throat patch (dthp), and double caudal chevron (cc), bounding the peduncle blaze (pb). Note also the thin anterior extension of the flank infill (fi), as a fine swirl, in the form of a Salvador Dali moustache. The underside of the tail flukes is in shadow and appears dark; most of the underside of the flukes is actually ivory white, as on the ventral field, with a dark grey trim at the tips of the flukes and onto the trailing edge of the flukes.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the contrast in the black and white photographs to that in the colour originals (i.e. to ensure that the contrast of dark and light grey areas were not enhanced). References are given to published illustrations to either illustrate another variation or, more usually, to establish the generality of the pattern.

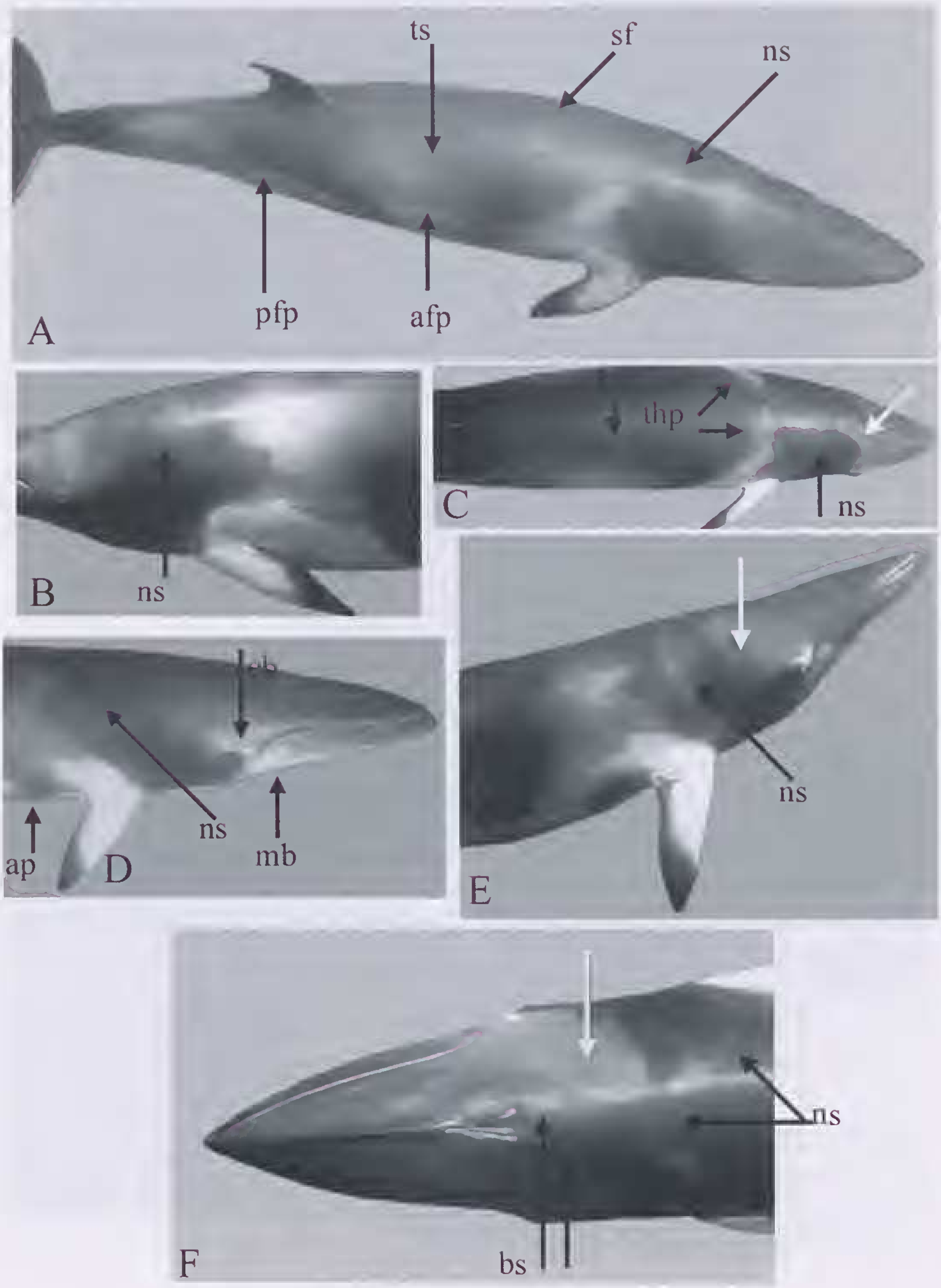
We rely largely on published descriptions and images for other mysticete species. Only photographs are used as evidence; although there are some excellent paintings (e.g. Foster in Leatherwood & Reeves, 1983) most illustrations of rorquals appear to be overly diagrammatic. This appears to be particularly true in illustrations of the common minke whale, and applies even to the most recent field guides (e.g. Folkens et al., 2002). Photographs of stranded whales may be from angles which obscure some of the colour patterns and often suffer from post-mortem darkening. Surface photos used for photo-ID's are especially valuable, but they show only the upper back of the animal. Underwater photographs are potentially the most useful but colour patterns may be obscured through extreme wave-refracted light creating dappling effects on the whales (e.g. sei and minke whales in Williamson, 1972, pls 1-3), through loss of contrast (e.g. fin whale in Cousteau, 1972: 50-51), or from angle of the shot (fin whale in Clapham, 1997: 46). There are additional problems with identification of the species in some publications (e.g. the photograph of a 'finback' whale in Cousteau (1972: 48) appears to be a Bryde's whale). The end result is that the documentation of particular colour elements may be based on photographs of a very small number of individuals. Within *Balaenoptera*, this is particularly the case for the Bryde's whale species complex and *B. omurai* Wada et al., 2003. While the appearance of a colour element in a photograph can be adequate proof for its existence in a particular species, failure to find it in photographs does not necessarily mean it is absent. It is thus difficult to generalise about colour elements in several species, a point that needs to be remembered when discussing phylogenetic significance of colour patterns.

The phylogenetic analyses were run using PAUP v. 4.0b10. Colour coding for the dwarf minke whale is based on new observations documented herein and a review of the literature. Colour coding for other species is based on the literature (Appendix). Insufficient information on the Bryde's whale complex or *B. omurai* was available to include any representative in the analyses. An exhaustive search was conducted. *Physeter* was set as the outgroup, based on phylogenies (Messenger & McGuire, 1998; Nikaido et al., 2001) which place the physeterids as a basal odontocete group.

COLOUR PATTERN OF DWARF MINKE WHALE

The dwarf minke whale has a dark grey back and ivory white underside (ventral field). The lateral colouration is much more complex with three dark grey fields descending from the back, white blazes ascending from the ventral field and a series of light grey patches, saddles and streaks. Together, these constitute the most complex colouration in any mysticete. The various colour

FIG. 2 (facing). Dorsal colour elements. A, The light grey of the rostral saddle (rs) extends further posteriorly on the right side of the body and is better defined than on the left. The two light grey blowhole streaks (bs) are clearly defined; the left blowhole streak curves to the left, a consistent feature in dwarf minke whales. The thin dorsal portion of the nape streak (ns) extends further forward on the left side of the body. B, The posterior edge of the right rostral saddle (rs) is markedly concave or scalloped by an antero-lateral extension of the dark nape field (nf). The white arrow points to a lateral ridge on the right side of the upper jaw. Lateral rostral ridges have been considered a feature of Bryde's whales but occur in some individual dwarf minke whales. C, The complex contour of a nape streak (ns) is seen in this whale; the nape streak expands into a diffuse patch on the left side of the animal. Note also the left curve of the left blowhole streak, the more posterior extension of the right rostral saddle and two lateral ridges (one on either side of the median rostral ridge). D, The posterior margin of the right rostral saddle is convex, a dark chain-like scar runs through the middle of the right rostral saddle. The nape streak continues onto the side as a thin convex line, mirroring the smooth curve of the anterior margin of the light grey thorax patch. The white of the ventral field extends upwards onto the base of the lower jaw as a mandible blaze (mb); the anterior half of the eyelids is also white, forming an eye blaze. E, The thin transverse nape streak (ns) angles back sharply before continuing down the side of the body. There is a healing oval scar on the nape streak.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elements are detailed below, progressing from the head posteriorly.

DARK FIELDS. *Spinal field (sf)*. This dark grey field on the dorsal surface (Figs 1A, 3A) overlays the occipital region of the skull and the whole vertebral column; it is called the spinal field, as in delphinids (e.g. Mitchell, 1970). It extends furthest forward along the midline of the back, just posterior to the blowholes, where it usually forms a dark background to the blowhole streaks (Fig. 3F; Clapham, 1997:60; Chadwick & Nicklin, 2001: 61). The spinal field extends downward on either side of the body as (1) a nape field continuing ventrally as a dark throat patch, (2) thorax field and (3) peduncle field (see below for details). It is usually at its narrowest above the flank patch just in front of and just behind the dorsal fin (Figs 3A,6B).

Nape field (nf). This dark band descends from the spinal field and continues ventrally as the dark throat patch. It is bordered anteriorly by the light grey rostral saddle, and posteriorly by the light grey thorax patch and white shoulder blaze (Figs 2B, 2D, 3B, 3D, 5A, 6B; Paterson, 1994, fig 2, lower; Hoelzel & Stern, 2000: 14, 26; Chadwick & Nicklin, 2001: 58-59).

Dark throat patch (dthp). All dwarf minke whales had a dark extension of the nape field extending onto the throat region from under the level of the eye to the anterior insertion of the flipper (Figs 1B, 1C, 5A, 7; Arnold et al., 1987, fig. 3a,e). It is particularly obvious when the throat is expanded. The development of the throat patch was asymmetrical on some individuals, extending further ventrally on the left side, but is not consistently so.

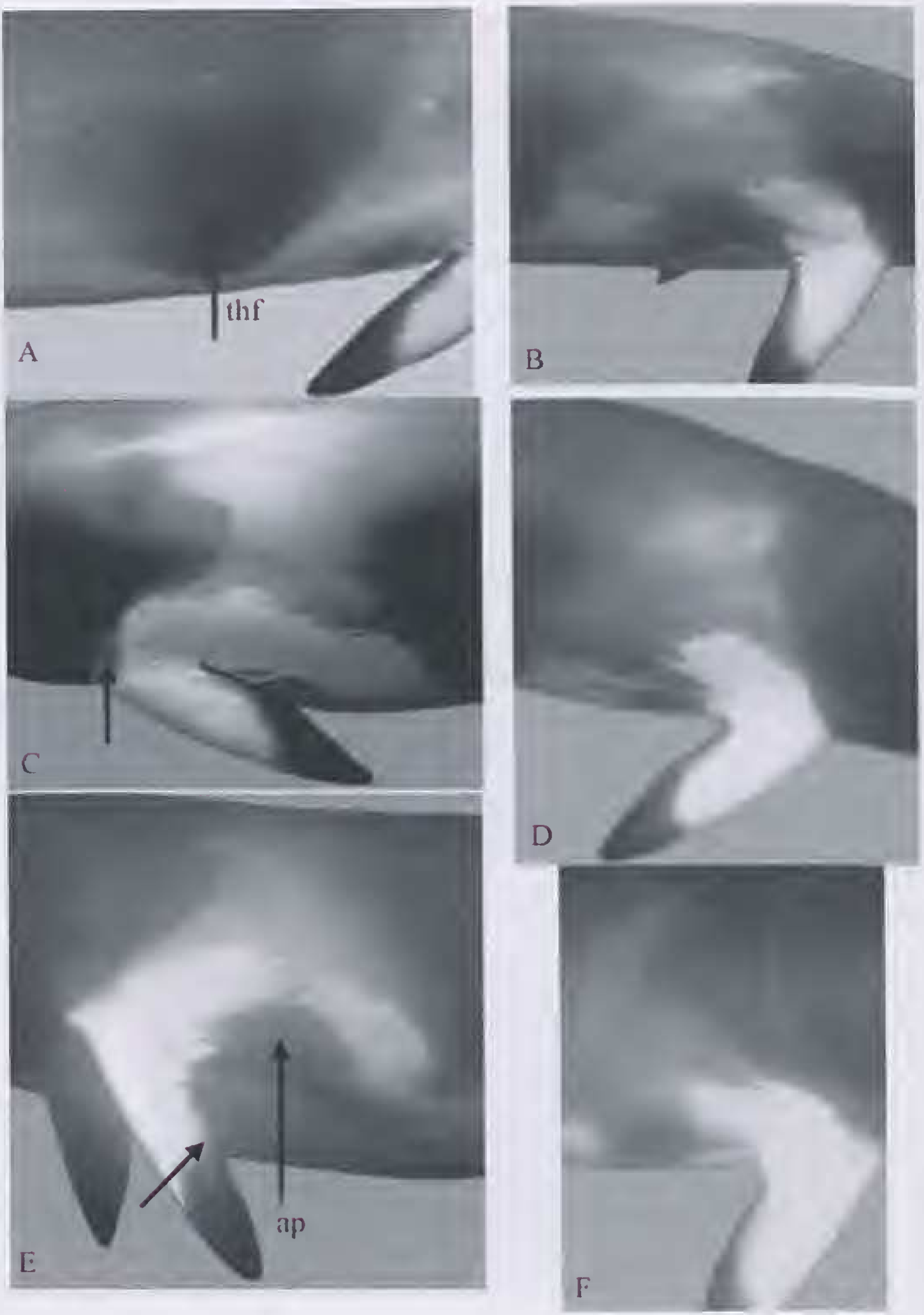
Thorax field (thf). This cape-like field descends from the spinal field and usually forms an inverted triangle, although in some individuals it is very narrow and vertically elongate. It is bordered anteriorly by the light grey thorax patch and posteriorly by the more variable, but generally light grey coloured flank patch. It may be a broad triangle with a truncated (Fig. 5C) or broadly rounded ventral margin (Figs 1C,3E), or thin with a more acute tip (Fig. 1A, 3A). The ventral margin of the thorax field may form an anteriorly directed hook (Fig. 1B); very occasionally the margin is bifurcated with both an anteriorly and a posteriorly directed hook.

Peduncle field (pf). Posterior to the flank patch and extending to the insertion of the flukes is a dark grey field which extends over all of the sides of the peduncle and well onto the ventral keel of the peduncle (Figs 1A, 3A, 5A).

Caudal chevrons (cc). The anterior margin of the peduncle field descends vertically onto the ventral field, then angles sharply forward, forming the posterior caudal chevron. The anterior caudal chevron, similarly angled, is a dark overlay extending from the flank patch onto the ventral field (Fig. 1B, C; Arnold et al., 1987, fig. 3c). In a few cases, the ventral portion of the chevrons may be detached from flank patch (*acc*) or peduncle field (*pcc*) by extensions of the ventral field, forming small detached dark patches.

WHITE FIELDS/BLAZES. *Ventral field (vf)*. This ivory white field covers the whole underside of the body, from the throat to the underside of the tail flukes (Figs 1B,1C). It is most extensive on the throat (except where it is partly infilled by

FIG 3 (facing). Dorsal and lateral colour elements. A, The dark grey spinal field (sf) extends along the back from the rostral saddle to the tail stock or peduncle; it is narrowest behind the dorsal fin where there is a dorsal extension of the posterior flank patch (pfp). The dark spinal field and posterior margin of the dark thorax field extend onto the anterior flank patch (afp) in a series of parallel dark "tiger stripes" (ts). The nape streak (ns) is thin throughout and extends down the right side to insert on the base of the flipper. B, The nape streak (ns) forms a diffuse patch (cf. the thin line shown in 2A). C, Diffuse extensions of the right and left thorax patches (thp) extend onto the back where they almost meet in an anteriorly directed peak, just to the left of the mid-line of the back. This takes the form of a nape streak but the actual nape streak (ns) can be seen in its usual position. The white arrow indicates the rostral saddle, with a strongly concave or scalloped trailing edge. Tiger stripes are clearly visible on the flank patch. D, The white ventral field extends upwards as a mandible blaze (mb) while the anterior half of the eyelids is white as an eye blaze (eb). The thin nape streak (ns) continues to the base of the flipper. The axillary patch (ap) is extensive and broadly attached to the thorax patch (see Fig. 4F for more detail). E, The posterior edge of the rostral saddle (white arrow) is straight. The nape streak (ns) bifurcates on the right side, with one branch directed posteriorly to join the anterior margin of the thorax patch, while the second branch continues to the base of the flipper. Note the broader, more anteriorly directed peak of the thorax patch (cf. D). The axillary patch is separate ("detached") from the thorax patch (cf. 3D). F, The right side of the rostral saddle (white arrow) extends further posteriorly and is more sharply defined than on the left side. The blowhole streaks (bs) are sharply defined, with the left blowhole streak curving to the left. The nape streak (ns) extends further onto the left side of the body.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the dark throat patch), the thorax and most of the abdomen. It narrows on the peduncle or tail stock where it is restricted to the ventral keel of the peduncle, before expanding to cover most of the flukes (Fig. 1C). The ventral field extends upwards onto the sides of the animal as (1) a mandible blaze (usually present on the right side of the body but only rarely on the left), (2) the shoulder blaze and (3) the peduncle blaze. The white of the ventral field may extend as splashes or streaks of white superimposed on the grey flank patch, which are particularly obvious when the flank patch is largely infilled by dark grey pigment.

Mandible blaze (mb). The whole of the left mandible margin is usually a dark grey colour, completely infilling the angle of the lower jaw (Figs 1B, 7A; Hoelzel & Stern, 2000: 23). On the right side, the white ventral field of the throat usually extends upwards on the angle of the lower jaw, sometimes almost on a level with the eye, as a mandible blaze. This colour asymmetry is particularly obvious on stranded animals, in which the muscles of the lower jaw have relaxed (Fig. 7B) showing much of the gape as lightly coloured. It is less obvious, but distinct, in living animals (Figs 2D, 3D,5A; Hoelzel & Stern, 2000: 26; Chadwick & Nicklin, 2001: 58-59, 66-67) in which the muscles adduct the lower jaw tightly against the rostrum (Lambertsen et al., 1995).

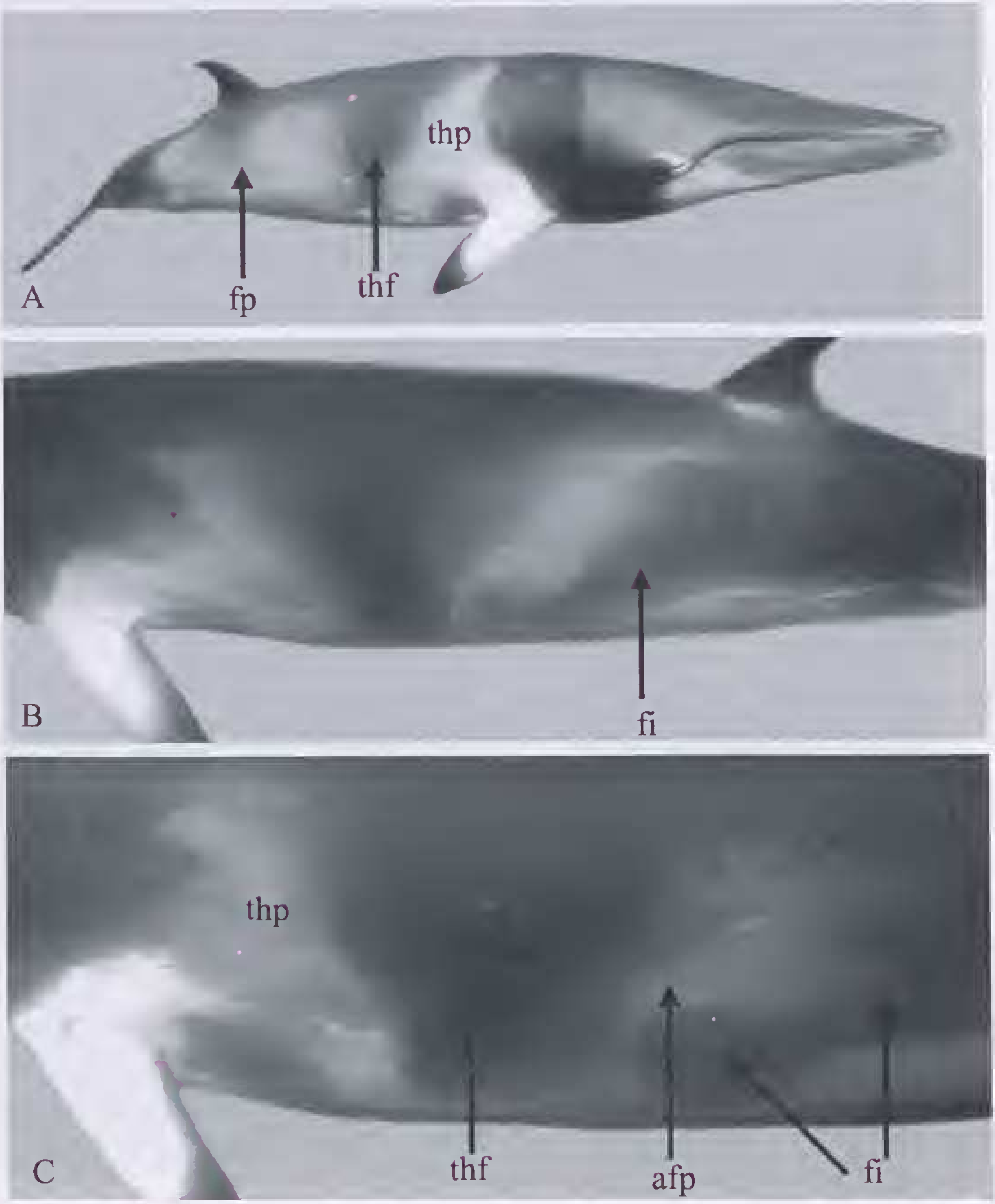
Eye blaze (eb). On the right side, white patches often occur over the anterior eye region and/or above the eye and may extend posteriorly to cover the entire region. Although most often covering just the anterior eye region (Figs 2D,3E, 5A), at its most extensive the white can cover most of both eyelids (palpebrae) as well as the dorsal and ventral folds (Figs 2D,3E; Hoelzel & Stern, 2000: 26 (nearer whale)). The eye blaze is usually absent from the left side of the body (compare right and left sides of whale in Fig. 7) but in those rare animals where an eye blaze is present on the left, the extent is reduced compared with its right eye blaze which is usually particularly well developed.

Shoulder blaze (shb). The shoulder blaze is bright ivory white; it occurs above the insertion of the flipper (Figs 1-7). The shoulder blaze is visible in all underwater photographs, even those in which the animal is distant (Fig. 1B; Laboute & Magnier, 1979: 136; Martin, 1990: 78 lower left). However, it often flares out because of the contrast with the predominantly grey animal. In photographs of stranded animals (e.g. Baker, 1983; Best, 1985), however, it may not always be possible to clearly separate the white shoulder blaze from the grey thorax patch above it. The shoulder blaze may merge posteriorly with an antero-dorsal extension of the ventral field so that the entire thorax patch is edged ventrally with bright white (Figs 1B, 3B, 3E, 4A,4C), however more usually the posterior margin of the shoulder blaze is defined by a variably developed dark axillary patch (see below).

Peduncle blaze (pb). The vertical components of the posterior and anterior caudal chevrons define

FIG. 4 (facing). Lateral thoracic colour elements. A, The ventral margin of the dark thorax field (thf) is broad and truncate. The posterior margin of the thorax field extends onto the light grey flank patch as a series of parallel dark thin "tiger stripes". The axillary patch is small, just behind the flipper. It is clearly separated from the thorax patch by white of the shoulder blaze and an extension of the ventral field. The dark distal flipper patch continues as a thin band along the trailing edge of the flipper, joining with the anterior extension of the axillary patch. B, The axillary patch is broadly attached to the thorax patch, dividing the white shoulder blaze from the extension of the ventral field. The axillary patch is "stacked", with layers of dark pigment one above the other. The ventral part of the axillary patch extends forward to the axilla of the flipper. C, The anterior margin of the thorax patch is sharply indented, with a prominent anteriorly directed peak. The white shoulder blaze is extensive, with only a small dark axillary patch seen just behind the flipper. Thus the axillary patch is broadly detached, as in A. The arrow indicates a light grey shoulder which extends from the posterior margin of the nape field onto the base of the flipper (same individual as in Fig. 3B). D, The axillary patch is broadly attached to the thorax patch and is more loosely stacked, with the individual layers of the axillary patch more clearly separated. The thorax patch is broadly truncate dorsally, with an ill defined anteriorly directed peak. E, The axillary patch (ap) is lightly attached by thin light grey streaks from the thorax patch, which separate the shoulder blaze (anteriorly) from an extension of the ventral field (posteriorly). The arrow indicates a light grey border from the distal flipper patch, extending onto the white of the basal flipper blaze. The ventral margin of thorax field is hooked forward towards the axillary patch. F, The axillary patch is broadly attached (cf. the broadly detached axillary patch in 4A and 4C, which is very clearly separated from the thorax patch by the white shoulder blaze and a dorsal extension of the ventral field). The axillary patch extends forward to the axilla of the flipper where it links with the thin dark grey pigment along the trailing edge of the flipper. The peak of the thorax patch is narrow and directed antero-dorsally (same individual as in Fig. 3D).

an area of white on the ventral field which extends upward into the dark peduncle field as a peduncle blaze (Figs 1A, 1C; Arnold et al., 1987, fig. 3c). The peduncle blaze can be vertical, directly above and at almost right angles to the chevrons (Fig. 1A, 1C), or angled forward to varying degrees. It usually forms a well defined streak up the side of the peduncle (see Figs above), but more rarely may be more diffuse, expanding dorsally as a light grey patch.



SADDLES, PATCHES & STREAKS. *Rostral saddle (rs).* The whole rostrum, back to the level of the reduced blowhole guard, is a lighter grey colour, which contrasts distinctly with the dark nape region (Figs 1A,2A,2B,3F,5A,6B). The rostral saddle usually is divided into a distinct right and left field by a medial forward extension of the spinal field reaching to the level of the blowholes (Fig. 3F). The right field generally extends further posteriorly along the back than does the left (Figs 2A, 2C,3F,6B). A forward extension of the dark nape field often creates a sharply defined, distinctly scalloped or concave posterior margin of the rostral saddle on the right side (Figs 2B, 6B; Clapham, 1997: 60; Chadwick & Nicklin, 2001: 61); other variations include a more convex (Fig. 3F) or straight (Figs 2D,5A) margin. The posterior margin of the left rostral saddle is usually much more diffuse, blending into the nape field (Fig. 3B).

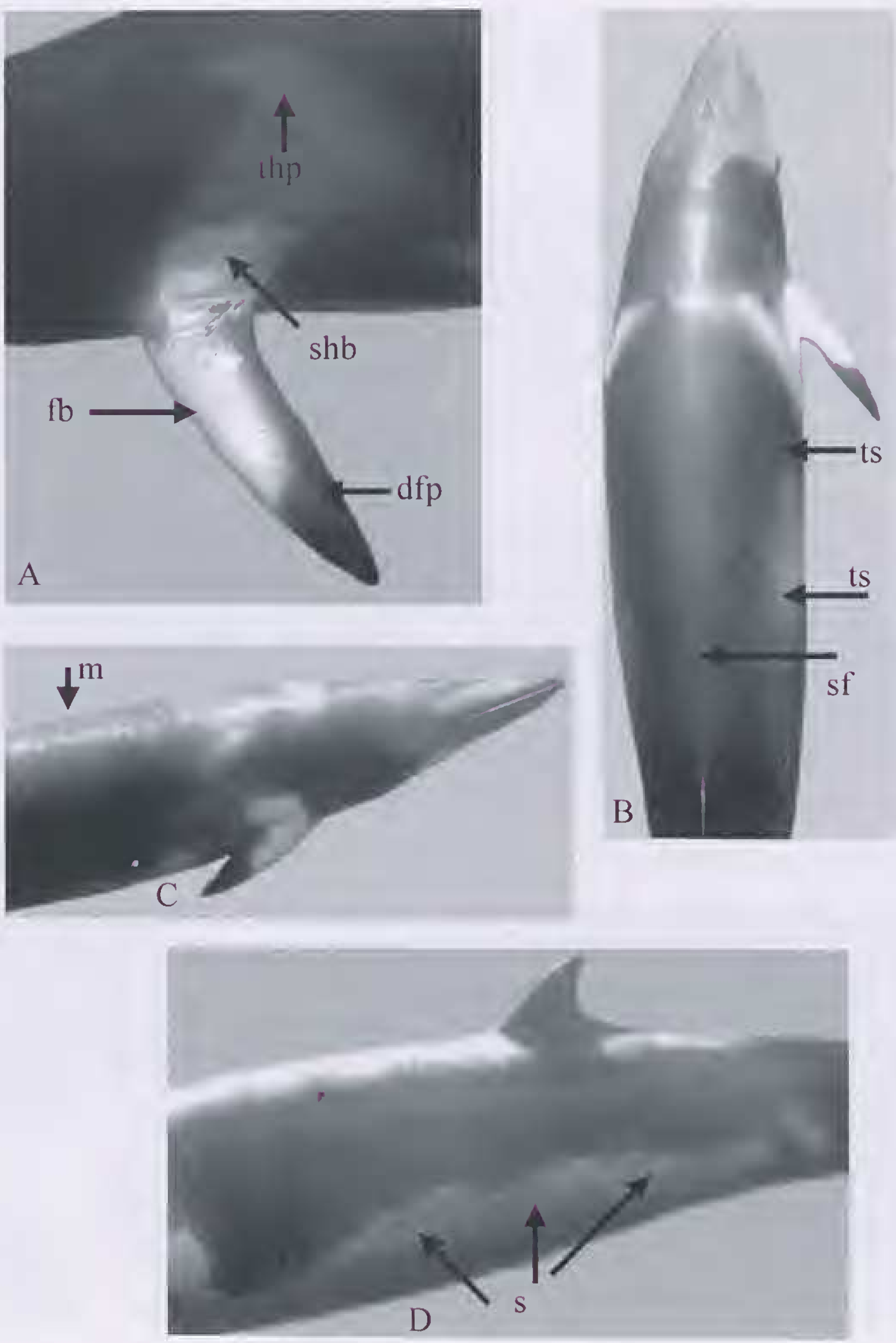
Blowhole streaks (bs). These light grey, thin lines originate from the posterior end of each blowhole slit. The right blowhole streak closely follows the medial margin of the right rostral saddle. It may run distinctly posteriad (Fig. 3F), but more frequently curves slightly to the left distally (Fig. 2C); in one animal seen in 2005 it diverged to the right. The left blowhole streak consistently and more strongly curves to the left (Figs 2A, 2C,3F,6B; Hoelzel & Stern, 2000: 14), generally running parallel to the convex posterior margin of the left rostral saddle (Fig. 3F; Clapham, 1997: 60; Chadwick & Nicklin, 2001: 61). We have seen no cases in which the left blowhole streaks ran to the right side of the body.

Nape streak (ns). Dorsally, the nape streak is usually a transverse thin light grey line against the darker background of the spinal field. It is always continuous across the back but is highly variable in form. The blaze can extend forward as a sharp peak on the midline of the body (Fig. 3A), form a straight line across the back (Fig. 2E), bow backwards in the midline (Clapham, 1997: 60) or be asymmetrical, extending further forward on the left side of the back (Figs 2A, 3F; Chadwick & Nicklin, 2001: 61). The nape streak often forms a sharp, almost right angle bend before descending down the sides of the nape field (Fig. 2E; Cox, 1989: 65; Hoelzel & Stern, 2000: 14; Chadwick & Nicklin, 2001: 58-59, 61). The individual shown in Chadwick & Nicklin (2001: 61) illustrates the sharp backward bend of the nape streak on either side of the back, however the pattern is somewhat obscured because the whole nape streak is shifted obliquely forwards and to the left, as is also the case in the whales shown in our Figs 2A & 3F. The dorsal portion of the nape streak may be sinuous (Fig. 2C), forming a complex pattern of grey on the spinal field and upper nape field.

Laterally, the nape streak continues down either side as a thin line (Figs 2A, 3A) or expands into a broad, diffuse grey patch which may be extensive (Figs 3B, 4C). The nape streak may angle sharply backwards about half way down the nape field and insert on the anterior margin of the thorax patch (Hoelzel & Stern, 2000: 26), continue ventrally to insert on the shoulder blaze just in front of the flipper insertion (Figs 2A, 2D,3A; Hoelzel & Stern, 2000: 6; Chadwick & Nicklin, 2001: 58-59) or bifurcate and insert on both these locations (Fig. 3E). The exact form of the nape streak is so variable that it can be used to recognise individual whales. However, the details are visible only on good video or photographs; indeed, the whole nape streak was missed by Arnold et al. (1987) in an earlier description of dwarf minke whales.

Ear stripe (es). This occurs only occasionally in dwarf minke whales. There is a fine line within

FIG 5 (facing). Flank colour elements. A, The thin cape-like thorax field (thf) divides the lateral light grey pigment into an anterior thorax patch (thp) and an extensive flank patch (fp), which is undivided by a flank infill. Also evident are the mandible blaze, eye blaze, a right rostral saddle with straight posterior margin, a thin nape streak which continues to the base of the flipper and a vertical white pigment band between the flank patch and dark peduncle field, which is a continuation of the peduncle blaze. This individual is unusually light in colouration, with an extensive rostral saddle, broad thorax patch and well developed flank patch. Two oval scars occur near the posterior edge of the thorax field; a parasitic copepod (*Pennella* sp.) trails from the lower oval scar. B, The thorax field is extensive in this individual and a well developed flank infill (fi) covers most of the flank region, leaving only a narrow light anterior flank patch. The flank infill continues forward and curves upward as a swirl or wave. The small axillary patch is broadly detached from the thorax patch. C, Another individual with a broad thorax field (thf), which is truncate ventrally; a small anterior flank patch (afp) is bounded by the thorax field anteriorly and an extension of the flank infill (fi) posteriorly. The flank infill expands anteriorly as a knob-like dark pigment patch. Tiger stripes extend into the anterior flank patch. The axillary patch is lightly attached.


thp
shb
fb
dfp
A
ts
ts
sf
B
m
C
s
D

the nape field, apparently an ear stripe, in photographs of a dwarf minke whale stranded on Pukehina Beach, Bay of Plenty, New Zealand (unpubl. photo, S. Gibney) and we have seen it on a number of individuals from northeastern Australia.

Thorax patch (thp). This light grey patch is usually triangular, with its base defined by the white shoulder blaze and antero-dorsal extension of the ventral field (Fig. 4C), and/or a variably developed axillary patch (see below). The anterior margin of the thorax patch is defined by the dark nape field. This anterior margin is sharply defined, and may be broadly concave (Fig. 4D) or sharply angled (Figs 4B, 4E), with an anteriorly directed peak (Fig. 4B). The dorsal border of the peak can be smoothly curved (Fig. 4E) or more flat and truncated (Fig. 4D; also compare animals shown in Chadwick & Nicklin, 2001: 66-67). The peak of the thorax patch generally extends higher on the right side of the body (Figs 5A, 7B) and may even extend across the midline of the back. The peak on the left side is usually lower and directed more anteriorly (Fig. 7A) but, rarely (Fig. 6B), may also extend medially so that right and left thorax patches almost meet on the back. The posterior margin of the thorax patch is defined by the thorax field; this edge may be diffuse, expanding as an indistinct cloud-like patch towards the midline (Figs 2A, 4B; Hoelzel & Stern, 2000: 14, 23 (same animal from different angles); Chadwick & Nicklin, 2001: 58-59).

Axillary patch (ap). Arnold et al. (1987) described a dark patch within the shoulder blaze which was completely surrounded by white; they called this the 'flipper oval' (Arnold et al., 1987, fig. 1). Subsequent field observations show that this 'flipper oval' is just one variation in the general shoulder region pigmentation. A dark patch is always present, though sometimes reduced in size (Fig. 4C). It may be completely separated dorsally from the thorax patch ('detached') and thus is completely surrounded by the white of the shoulder blaze merging with an extension of the ventral field (Fig. 4C; Cox, 1989: 65; Hoelzel & Stern, 2000: 14, 23 (same animal)); narrowly attached to the thorax patch (Figs 4E, 5C; Arnold et al., 1987, fig. 3c) or broadly attached to the thorax patch (Figs 1A, 2D, 3D, 4B, 4F, 6A; Chadwick & Nicklin, 2001: 58-59, 66-67). In the last case, the dark patch largely infills the extension of the white ventral field so that the only major area of white is the shoulder blaze above the insertion of the flipper (Fig. 6A). A broadly attached axillary patch looks like an extension of the thorax patch (Figs 1A, 4F). The patch may be entire and broadly rounded (Fig. 5C) or may be more acute anteriorly and posteriorly, so that the patch appears to be broadly bifurcated (Fig. 4B). In other cases, the margins of the dark patch may be deeply serrate, appearing as a vertically "stacked" series of dark bands (Fig. 4B). In some animals these may be reduced so that they are separated from each other or even so reduced as to form one or two small oval blotches one above the other in the ventral field (Fig. 4D).

The dark patch (or at least one of the patches in the rarer cases when there is more than one patch on the ventral field) runs forward to the axilla of the flipper and is generally continuous with the dark pigment running along the trailing edge of the flipper (Figs 3D, 3E, 4B, 4D-F; Best, 1985, fig 1c; Hoelzel & Stern, 2000: 14, 23). This can be clearly seen when the flipper is held out and downwards from the body (Fig. 4) but may not be visible in photographs of stranded animals, where the flipper is held closer to the body. Given its consistent occurrence at the axilla of the flipper, we suggest that a more general term for the dark patch in the shoulder blaze is 'axillary patch', which we propose should replace the term 'flipper oval'.

Flank patch (fp) and flank infill (fi). The generally light grey flank patch extends from the

FIG 6 (facing). Colour variations. A, An extensive axillary patch, broadly attached to the thorax patch (thp) reduces the extent of the shoulder blaze (shb) to an area just above the flipper base. The dark distal flipper patch (dfp) extends along the trailing edge of the flipper in a particularly broad band (cf. individuals shown in Fig. 4A-F) which extends forward into the white flipper blaze (fb) at the base of the flipper. A light grey shoulder extends from the nape field backwards onto the flipper blaze at the base of the flipper. This individual shows particularly extensive infilling of the flipper blaze. B, The dark spinal field (sf) is narrowest just before the dorsal fin due to a dorsal expansion of the flank patch. Well developed tiger stripes (ts) extend from the spinal field and posterior edge of the thorax field onto the flank patch (same individual as in Fig. 3C). C, Dark flecks or mottling (m) of the back may be pigment or due to flaking of the skin. This individual has a broadly attached, extensive axillary patch, reducing the extent of the shoulder blaze. D, Close-up of individual shown in Fig 1B, showing the streaks and speckling (s) from the dark flank patch on to the white ventral field.

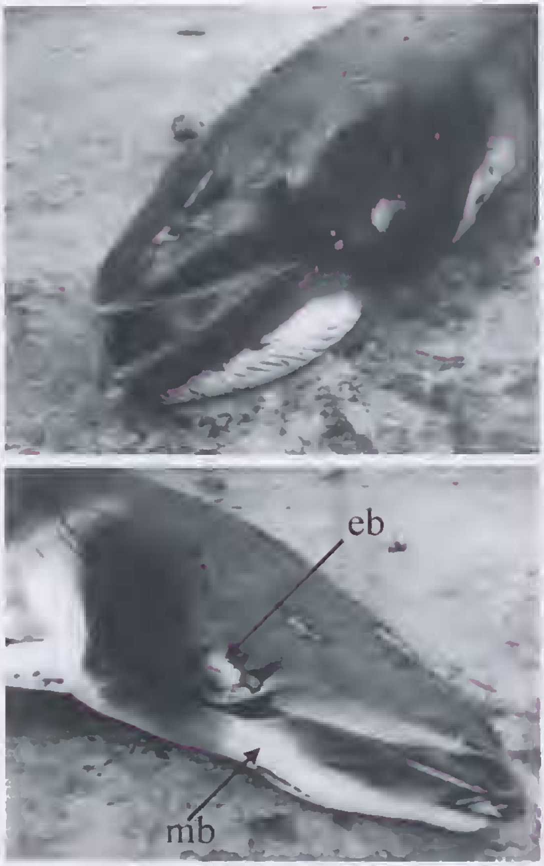


FIG. 7. Dwarf minke whale stranded at Lady Elliot Island, showing characteristic asymmetry. There is a mandible blaze (mb) and eye blaze (eb) on the right side but the mandible is completely dark on the left side, with no eye blaze (the white behind the eye is an abrasion). The dark border of the left mandible is continuous with the dark throat patch, making the left side appear distinctly darker than the right side of the head and shoulder region. The thorax patch extends high up the right side, while it is lower and angled more strongly forward on the left side. There is a less obvious demarcation of the white shoulder blaze and light grey thorax patch than in photographs of living dwarf minke whales.

dark thorax field to the peduncle field. It is bordered ventrally by the white ventral field and can be almost entirely light grey (Fig. 5A), or variably obscured by the flank infill, which can vary considerably in size and shape. The most frequent infill is the anterior triangle (Fig. 1A). The apex of the triangle may form a broad, dorsally directed swirl (Paterson, 1994, fig 2, lower; Secchi et al., 2003, fig 1) or a more elongate, thin swirl with the fine tip, curled like a Salvador Dali moustache (Figs 1C, 5B). The curled tip may itself be infilled, creating a knob at the end of the swirl (Fig. 5C). Where infilling occurs, the flank patch is divided into an anterior flank patch and posterior flank patch (Fig. 1A: *afp, pfp*). Cox (1989: 65) illustrated major infilling, with only a small anterior flank patch in front of the dorsal fin; similarly extensive infilling is shown in Fig. 5B, C. The most extensive infilling obscures most of the flank patch so the ventral field is edged with darker grey, which make any dorsal splashes or swirls from the white ventral field or speckling and streaking (Figs 1B, 6D) stand out.

Tiger stripes (ts). These parallel, dark, usually vertical stripes extend from the spinal field and thorax field onto the flank patch. They may occur on the anterior margin of the thorax field in which case they extend downwards onto the thorax patch (Figs 3C, 5C, 6B) or they may extend from the ventral margin of the thorax field onto the white ventral field.

Speckling (s). Speckling or streaking can occur particularly along the lower edge of the flank patch or on the adjacent margin of the ventral field (Figs 1B, 6D). This can be grey pigment against the white of the ventral field or white pigment on the grey of the flank patch.

Mottling (m). The dark grey of the spinal field, upper nape field and thorax field, as well as the dorsal fin and upper sides of the flukes, may contain patches of light grey mottling of variable size and shape (Fig. 6C). These light patches do not appear to be distinct colour elements but may reflect a condition of the skin (e.g. patches which are about to be, or have recently been, sloughed).

FLIPPER. *Flipper blaze (fb).* The base of the flipper is consistently filled by a white blaze (Figs 1-7). The white is most extensive on the anterior half of the flipper, occupying about two thirds of the flipper length as seen from above, with the white continuing along most of the leading edge of the flipper.

The insertion of the flipper is predominantly white (Figs 1A, 2A, 3D, 3E, 4B-F). There are individual variations in the amount of speckling and/or dark patches over the white flipper blaze (compare Figs 2A & 2B). Usually the light grey of the thorax patch extends ventrally along the posterior margin of the nape field and onto the base of the flipper, forming a light grey shoulder of variable size and shape (Figs 2B, 4C). Rarely (Fig. 6A; Kato & Fujise, unpubl. data) this light

Table. 1. Coding for phylogenetic analysis. Numbers in bold in the first row indicate the characters used (1: rostral saddle, 2: blowhole streaks, 3: dark nape field, 4: form of dorsal portion of nape streak, 5: ventral nape streak, 6:ear stripe, 7: basal flipper colouration, 8: distal flipper colouration, 9: axillary patch, 10: thorax field, 11: caudal chevron, 12: peduncle streak, 13: asymmetry). See Appendix for basis of character coding.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Physeter	0	0	0	0	0	0	0	0	0	0	0	0	0
Balaena	0	0	0	0	0	0	0	0	0	0	0	0	0
Eubalaena	0	0	0	0	0	0	0	0	0	0	0	0	0
Caperea	1	0	1	1	0	0	0	0	0	1	0	0	0
Eschrichtius	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaptera	0	0	0	0	0	0	0	0	0	1	0	0	0
B. musculus	0	0	2	0	0	0	1	1	0	0	0	0	0
B. physalus	2	1	1	1	1	1	1	1	1	2	1	0	2
B. borealis	1	1	1	1	0	1	0	0	1	2	0	0	1
B. bonaerensis	0	2	1	1	1	1	3	1	1	3	2	1	1
Dwarf minke	2	1	1	2	0	1	2	2	2	3	2	2	1
B. acutorostrata	1	1	1	2	0	1	3	2	1	3	2	2	1

grey shoulder of the thorax patch extends posteriorly towards the axillary pigment, which together may create an interrupted thin grey strip across almost the entire width at the base of the flipper. The dark nape field may also extend onto the base of the flipper; at certain angles this suggests that at least part of the base of the flipper is dark (Fig. 2A). However, none of the infillings of the flipper base approaches the dark base in the common minke whale or the type 2 flippers of the Antarctic minke whale (Appendix).

Distal flipper patch (dfp). The distal part of the flipper is covered by a dark grey patch (Figs 1-7), edged proximally with a light grey border (Fig. 4E). There are individual variations in the extension of this light grey border of the dark flipper patch, often forming streaks or patches extending onto the white flipper blaze (Figs 2B, 3E, 4E, 6A).

The proximal margin of the dark flipper tip runs obliquely backwards so that the entire rear margin of the flipper to the axilla has a dark grey edge (Figs 3E,4D,4F; Chadwick & Nicklin, 2001: 58-59). This dark margin is generally continuous with the axillary patch. The dark flipper patch can be seen on the underside of the flipper (Fig. 1C), which also mirrors the more extensive distribution of white along the anterior half of the flipper.

The overall colour pattern of the flipper is remarkably consistent in the >200 different individuals on which this paper is based, and in the photographs of animals from South Africa, New Zealand, New Caledonia and Brazil (Baker, 1983; Best, 1985; Cox, 1989: 65; Laboute & Magnier, 1979; Martin, 1990: 78; Zerbini et al., 1996; Secchi et al., 2003).

PHYLOGENETIC ANALYSIS

The colour coding is given in Table 1. Given that the Antarctic minke whale exhibits two pigment types, type 1 (monotone) flipper and type 2 (two-tone) flipper, two analyses were done with basal flipper colour coded 1 and 3 respectively. In the first analysis, an exhaustive search returned a single tree (Fig. 8) with a consistency index of 0.839 and a rescaled consistency index of 0.743. With the flipper base coded 3, the same tree was recovered, with a consistency index of 0.839 and rescaled consistency index of 0.886. The transformation series given below refers to the first analysis only.

The common and dwarf minke whales were united by the following characters: dorsal and lateral nape streak linear or diffuse (not V-shaped), ventral nape streak (Appendix, section 5) absent, distal flipper patch present (and white flipper blaze variably developed), and peduncle blaze well developed. The last character may not be consistent as the peduncle blaze and white up the side was clearly visible in only one photograph of a common minke whale (Norris & Prescott, 1961 (Appendix, section 12)). However the other characters represent well defined and consistent (hence diagnostic) synapomorphies in the nape streak and flipper, separating both common and dwarf minke whales from the Antarctic minke whale.

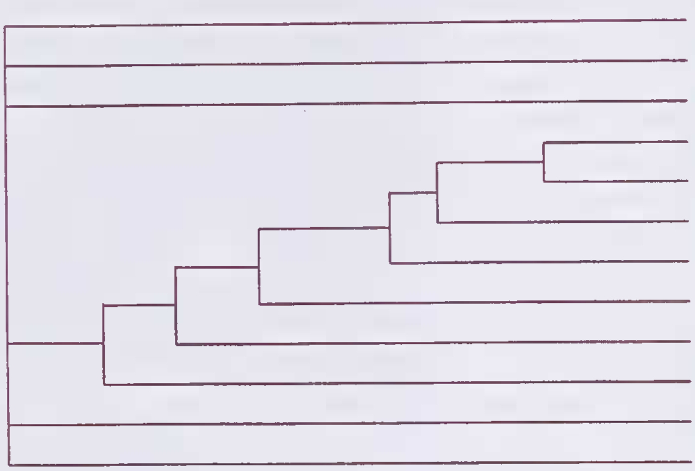


FIG. 8. Cladogram based on 13 colour elements (see Table 1 and Appendix for details).

The common, dwarf and Antarctic minkes were united based on a double caudal chevron, a peduncle blaze in the ventral field, and a cape-like dark thorax field, separating the grey of the sides into a distinct anterior thorax and posterior flank patch. The peduncle blaze is partially a correlate of the double chevron, which defines an area of white separate from the rest of the ventral field of the caudal peduncle. However, the double caudal chevrons and thorax field represent well supported and consistent synapomorphies of all the minke whales.

The minke whales and fin whale were united based on at least one caudal chevron (one in fin, two in the minkes); a ventral nape streak (shared only by fin and Antarctic minke whale) and uniform coloured flipper base and tip, with white leading edge (shared only by fin and Antarctic minke whale). This grouping was poorly supported with reversals of colour characters in the dwarf and common minke whales.

The minkes, fin and sei whales were united as a general *Balaenoptera* clade, united by colour asymmetry (though this is strongly developed only in the fin whale and at least some individuals of Bryde's whales and *B. omurai*), grey along the sides of the body (versus uniform or black and white colour of more basal taxa), blowhole streaks, ear stripe and possibly axillary patch (best defined in minke whales, and especially dwarf minke whale). Table 2 shows the distribution of colour elements in *Balaenoptera* species. *B. omurai* is not included because its colour pattern is insufficiently known. The taxonomy of the Bryde's whale complex is unresolved, therefore colour elements documented in the literature may refer to more than one species. Thus "Bryde's whales" were excluded from the cladistic analysis, however some information on one population is included in the Table based on underwater video (BBC: *Wild Australasia: Southern seas* and by Peter Constable) of individuals taken at Turtle Bay, Dirk Hartog Island, Western Australia (see Appendix for more details). Table 2 indicates that blowhole streaks and an ear stripe occur in at least some individuals of fin, sei, Bryde's, common, dwarf and Antarctic minke whales, though they may be too inconsistent to be diagnostic. The light grey lateral field occurs in all but the sei whale. A light grey flipper, with light grey to white leading edge, occurs in all *Balaenoptera* species except the sei, common and dwarf minke whales (though the white of the flipper blaze is most extensive anteriorly in the last two species). Colour asymmetry (with the right side lighter) is variably developed but has been reported in at least some individuals of fin, sei, Bryde's, Antarctic and dwarf minke whales, as well as *B. omurai*. The common minke whale may also be asymmetrical (the rostral saddle appears to be better developed on the right side of an individual illustrated in Hoelzel & Stern, 2000) but there is

Table 2. Colour characters of mysticete whales. The colour characters for Bryde's whales are based on video of whales from Western Australia and relate only to that population. Question marks indicate that there is no information in the literature or that the evidence is especially equivocal. In the last row (Asymmetry), 'C' indicates that there is consistent asymmetry, + indicates that asymmetry has been documented in at least some individuals and ?, as above, indicates that information is unavailable or equivocal for the taxon (or, in the case of "Bryde's whale", Western Australian population) used for coding. Abbreviations include bowh=bowhead, humpb=humpback, Brydes (WA)= Western Australian population of Brydes whale species complex, omurai= *Balaenoptera omurai*, Antarc= Antarctic.

	sperm	right	bowh	pygmy right	gray	humpb	blue	finback	sei	Brydes(WA)	omurai	common minke	dwarf minke	Antarcminke
Rostral saddle				+				+	+		+	+	+	
Nape streak				+				+		+	?	+	+	+
Blowh Steak								+	+	+	?	+	+	+
Ear stripe								+	+	+	?	+	+	+
Lateral field				+				+		+	?	+	+	+
Light distal,white leading edge							+	+		+	+			+
Asymm							?	+C	+	?	+	?	+C	+

insuffieient information in the literature to determine asymmetry/ symmetry of eolour in that taxon.

The "*Balaenoptera*" elade and *Caperea* were united based on a rostral saddle, defining a dorsal nape field, plus a V-shaped dorsal nape streak.

Megaptera was united with *Balaenoptera* and *Caperea* based on a blaek or dark grey and white eolour pattern (as opposed to the uniform eolouration of more basal taxa).

The blue whale was separated from the other balaenopterids, while *Eubalaena, Balaena* and *Eschrichtius* showed no variation from the outgroup *Physeter*.

DISCUSSION

COLOUR PATTERN VARIATIONS. Best (1985), based primarily on speeimens from South Afriea, documented a 'diminutive form' of minke whale with an unusually large proportion (relative to Antaretie minke whales) of light baleen plates, a white flipper base (our "flipper blaze") eonfluent with a white shoulder pateh (our "shoulder blaze") and dark pigment in the neek region extending onto the ventral grooves (our "dark throat pateh"). He was able to identify one or more of these features in speeimens from Australia, New Zealand and Brazil. Arnold et al. (1987) eonfirmed all these features in 14 speeimens from eastern Australia and extended the detail of the eolour pattern deseription. They noted the elear separation in eolour patterns between the dwarf and 'ordinary' form (now reeognised as *B. bonaerensis*) and argued that they were taxonomieally distinet. However at that stage material was insuffieient for a formal deeision.

The present paper greatly extends the sample size (>200) for Australian waters and ineorporates new information from New Zealand, Vanuatu, Fiji and Brazil. It eonfirms that the eolour patterns identified by Best eo-oeeur eonsistently over the whole southern hemisphere range of dwarf minke whales. There may be eonsiderable variation in the development of the axillary pateh of dwarf minke whales and a eorresponding ehange in the extent of the shoulder pateh. Infilling of the flank pateh is also variable and can produee eonsiderable differenees in the darkness of individual whales. None of this variation ehanges the faet that the eolour elements reeognised by Best (1985) and Arnold et al. (1987) are eonsistent.

The elear separation in the eolour patterns of dwarf and Antaretie minke whales is also maintained with the larger sample size, with no evidenee of intermediate eolour patterns between the two taxa. Off South Africa, there is evidence that dwarf and Antarctic minke whales occur in different habitats, with the dwarf minke whale occurring in more coastal waters (Best, 1985). The separation is not absolute, however. Kasamatsu (1988) documented dwarf minke whales several hundred kilometres off the Western Australian coast in oceanic waters. On July 6, 2000, at Reef 15-040 (15°23.15'S. 145° 45.78'E), we were in contact with four dwarf minke whales which were briefly joined by an immature Antarctic minke whale. Such instances, however, are still exceptional, and there may sufficient ecological separation of dwarf and Antarctic minke whales to maintain a partial reproductive barrier. Intraspecific geographical variation, including distinctive colour patterns, is well documented in delphinid cetaceans, e.g. Commerson dolphin, with a distinctive disjunct population around the Kerguelen Islands (Pichler et al., 2001), Hector's dolphin with a subspecies restricted to the North Island of New Zealand (Baker et al., 2002), the 'truei' variant of Dalls porpoise (Amano & Miyazaki, 1996) and pilot whales off Japan (Kasuya et al., 1988). However, the consistent occurrence of the colour elements throughout the extensive range of the dwarf minke whale and the lack of intermediate colour patterns linking it with the Antarctic minke whale, despite their overlaps in occurrence throughout their ranges, contrast with the regional differences in colour patterns of the delphinids just quoted. This indicates that the dwarf minke whale and Antarctic minke whales are reproductively isolated and thus supports their status as distinct species. The colour features are sufficiently consistent to allow separation of dwarf and Antarctic minke whales in the field, at least if they are seen under favourable conditions.

PHYLOGENETIC ANALYSIS. Whereas the colour pattern data can be used as evidence of reproductive isolation between the sympatric to parapatric populations of dwarf and Antarctic minke whales, taxonomic inferences are more difficult in the case of the allopatric populations of dwarf minke whale and the common minke whale.

Using a combination of osteological, limited morphometric and colour pattern data, Arnold et al. (1987) suggested that the dwarf minke whale was more closely related to the common (northern hemisphere) minke whales than to the 'dark shoulder' or 'Antarctic minke' (*B. bonaerensis*), a view already anticipated by Best (1985). This was based on a limited sample size but, more importantly, was essentially phenetic without an indication of possible phylogenetic features.

The diagnostic features of the dwarf minke whale (dark throat patch, shoulder blaze, white flipper blaze) are autapomorphies and thus of no phylogenetic significance. In this paper, we present a cladistic analysis based on 13 other colour elements which show a greater potential to establish taxonomic relationships. It must be noted that the resulting cladogram poorly reflected the presently recognised families of baleen whales and contained no monophyletic groups. Nonetheless, the analysis did suggest several taxonomic relationships.

In our analysis, the common and dwarf minke whales were united based on their more specialised flipper colouration (diverging from the more general pattern of a uniform dorsal pigment with a light grey to white leading edge as found in Antarctic minke whales), more specialised nape streak (linear to diffuse, in contrast to the more generalised V-shaped dorsal streak found in balaenopterids including the Antarctic minke whale), and the lack of a ventral nape streak element which creates the W-shaped chevron found in fin and Antarctic minke whales. The presence of these synapomorphies in colour elements provides evidence that the dwarf and common minke whales are sister taxa, sharing a more recent ancestry than either does with the Antarctic minke whale. This phylogenetic pattern is consistent with previous studies based on morphology (Best, 1985; Arnold et al., 1987; Zerbini et al., 1997) and molecular data (Wada & Numachi, 1979; Pastene et al., 1994).

All minke whales shared a set of specialised colour characters, primary of which is the separation of the lateral light grey field by a dark cape-like thorax field into an anterior thorax patch and a posterior flank patch, as well as the development of a double caudal chevron.

Finally there was a suggestion of a suite of colour elements which may be characteristic of most *Balaenoptera* species (Table 2). These include variably developed left-right colour asymmetry, blowhole streaks, ear stripe and generalised light grey pigment area along the sides of the body between the darker grey spinal field and white ventral field. It is often stated that the fin whale is the only consistently asymmetrical species. However a consistent, albeit more subtle, left-right asymmetry occurs in dwarf minke whales. Strikingly asymmetric individuals within the Bryde's whale species complex and *B. omurai* have also been documented (see Appendix, section 13). The uniformity of colour elements among sei, fin and all the minke whales provides no support for the separation of minke whales from other rorquals as suggested by Árnason & Gullberg (1994), based on cytochrome b gene sequences. However, except for possible asymmetry of colour and generalised flipper pigment in blue whales (Appendix), neither the blue whale nor the humpback whale show any of these colour elements. Such differences in colour have previously been attributed to differences in life style (either habitat and/or diet), e.g. the uniformly mottled colour of the blue whale has been linked to its obligate planktivory. However, this does not explain the lack of certain colour elements such as the V-shaped dorsal nape streak which is not present even in foetal blue whales (Mackintosh & Wheeler, 1929), in marked contrast to fin and sei whales (Mackintosh & Wheeler, 1929; Matthews, 1938) in which the streak is even more distinct in foetal whales than in the adult. Fossil evidence (Fordyce & deMuizon, 2001) indicates that the humpback whale diverged early from the other balaenopterids (Miocene, 11-12 million years ago) and it already has been placed in a separate genus (and even subfamily) based on morphological differences in the size of flipper and form of scapula. The lack of any of these "*Balaenoptera* colour elements" in the blue whale suggest that it may also represent a lineage which diverged early within the evolution of *Balaenoptera*. However, the relationships within balaaenopterid whales remain unresolved, including a recent molecular study (Rychel et al., 2004) which presented a range of different phylogenies depending on the molecular marker and type of analysis used.

At the highest levels, the phylogenetic signals within colour patterns appear weak. *Caperea*, which is generally placed in its own family, Neobalaenidae (Miller, 1923; Barnes & McLeod, 1984; Árnason & Gullberg, 1994) based on morphological and molecular data, was placed with the fin, sei and minke whales (all family Balaenopteridae), while other balaenopterids such as the humpback whale and blue whale were separated from this clade (Fig. 8). The more uniform colour patterns of the balaenids and gray whale (Eschrichtiidae) provided no evidence on the relationships of those taxa. Their similarity in colour elements to the outgroup, the sperm whale (as well as to many beaked whales), suggests that uniform colouration is the ancestral pattern for mysticetes.

TAXONOMIC IMPLICATIONS. Despite the lack of monophyletic groups, the phylogenetic analysis did provide support both for the close relationships of all minke whales, and particularly the common and dwarf minke whales. However it gives no indication of the taxonomic level at which the dwarf minke whale should be recognised (i.e. species or subspecies).

Within phylogenetic studies, any taxon which can be diagnosed is usually recognised as a species. However this merely represents a convention and it is hard to see how there can be an operational definition of a phylogenetic species when the technique depends on recognition of shared specialised features to establish common ancestry yet species themselves are diagnosed on the basis of autapomorphies which have no phylogenetic significance.

Even with molecular data, taxonomic differences are particularly difficult to infer when the compared populations are allopatric (Helbig et al., 2002; Milinkivitch et al., 2001). If, as suggested by Helbig et al. (2002), it is practically impossible to directly test the ability to interbreed in allopatric populations (e.g. dwarf and common minke whales, which occur in different hemispheres) then one wonders whether there can be an operational species definition based on the biological species concept. The biological species concept is further compromised by data (Bérubé, 2002) which suggests that finback and blue whales (whose species integrity is well supported by both morphological and molecular data) can hybridise.

Molecular analysis of minke whales by Goto & Pastene (2000) grouped common minke whales from the North Atlantic and dwarf minke whales, both of which were distinct from all samples of common minke whale from the western North Pacific. However, an analysis presented by Baker et al. (2000) linked the western Pacific common minke whales in one cluster, common minke whales from the North Atlantic in another cluster and the dwarf minke whale in a third cluster, as an unresolved trichotomy. This could be considered evidence that the western North Pacific common, North Atlantic common and dwarf minke whales are all phylogenetic species (Baker et al., 2004), clearly a different taxonomic hypothesis from that suggested by the data in Goto & Pastene (2000).

Mayr (1969) suggested that in doubtful cases of separation between allopatric populations, that the taxa be considered as subspecies. On this basis, we agree that the dwarf minke whale should be recognised as a subspecies of the common minke whale as suggested by Rice (1998), based on available information. We do not make any formal taxonomic decisions, as the status of the dwarf minke whale (as well as western North Pacific common minke whales, with an unresolved relationship to the nominal taxon *B. a. scammoni*, described from the eastern North Pacific) must eventually be decided based on the full range of characters and extent of concordance in osteological, morphological and molecular data from throughout the range of all the minke whale taxa. We do note, however, that there are consistent, diagnosable differences in the colour pattern of the dwarf minke whale which are more extensive than the colour pattern variations between the nominal subspecies of common minke whales (*B. a. acutorostrata, B. a. scammoni*) from the North Atlantic and North Pacific respectively. This suggests that the dwarf minke whale may warrant species rather than subspecies recognition.

ECOLOGICAL VERSUS PHYLOGENETIC BASIS FOR COLOUR PATTERN VARIATIONS. The possible influence of ecological factors should be noted. Brodie (1977) suggested the white flipper bands of northern hemisphere minke whales might be used in herding schooling fishes. Although the dwarf minke whale, also with white flippers, is known to feed on fishes (Kasamatsu et al., 1993), the 'herding hypothesis' does not explain the complex patterns of white, light grey and dark grey found in all minke whales.

Yablokov (1963, in Mitchell, 1970) contrasted three colour patterns: (1) uniform, which he associated with obligate planktivores or deep divers, (2) countershaded, which he linked to species feeding on nekton in the photic zone and (3) discretely bounded, which Yablokov linked to intraspecific signalling.

Minke whales in general, and dwarf minke whales in particular, have discrete pigment patches. There is evidence that common minkes of the north Atlantic, Antarctic and dwarf minke whales spend at least part of their life cycle in low latitudes where the water is clear (tens of metres) even in coastal areas and extremely clear (50-100m) in the open ocean. Dwarf minke whales are relatively small for a baleen whale so that the whole whale is clearly visible underwater and the colour elements – especially the white flipper base and shoulder blaze in dwarf minke whales – stand out right to the limits of underwater visibility (pers observations; also note photographs). In close contact (10-100m) visual signals have greater potential to identify individual whales than the vocalisations which are intense (Gedamke et al., 2001), essentially omnidirectional and thus difficult to localise. They could also be used in positioning and orienting to other whales collaborating in cooperative hunting manoeuvres. The complexity and strongly contrasting colour patterns in minke whales, especially the dwarf minke whale, is consistent with Yablokov's hypothesis and suggests that vision is an important sense when minke whales are close together.

Despite this behavioural 'overlay' there appears to be a phylogenetic basis for the variation in the colour elements, as indicated by the cladistic analysis. As in other groups of animals, the phylogenetically significant characters may not be the most obvious features of the whales and may be visible only in good photographs of living or very freshly stranded whales. For example, the blowhole streak was not recognised in any balaenopterid until 1985 when it was described in the Antarctic minke whale by Best (1985). It was initially missed in an earlier description of Australian dwarf minke whales (Arnold et al., 1987) and we also document it for the first time in the common minke whale in the present paper, based on photographs of live animals (e.g. Hoelzel & Stern, 2000).

Such photographs are particularly limited for sei whales and any of the Bryde's whale complex, but even in relatively "well known" species such as fin whales, the colour patterns are only poorly documented. Ironically, within the minke whale complex, it is in the common minke whale of the northern hemisphere that colour patterns are most poorly documented. We hope that by making others aware that balaenopterid whales have a range of consistent colour elements, that those with the opportunity to take photographs of living whales will record such features. It is only with a better range of photographs that we will be able to check whether our interpretation of the literature is correct and thus test the validity of the taxonomic hypotheses suggested by our cladistic analysis.

The recognition that such features as colour asymmetry, V-shaped dorsal napestreak and rostral saddle may be more generally distributed within species of the genus *Balaenoptera* suggests that great caution is necessary in the identification of rorquals from field photographs, especially in the tropical Indo-Pacific with its complex of poorly known Bryde's whales. For instance, there seem to be greater similarities in the colour pattern of some Bryde's whales and the Antarctic minke whale than generally acknowledged in the literature (see, for example, photograph of a confirmed Bryde's whale in Baker, 1983). Resolution of these problems will require that good colour data, morphometrics, osteology and molecular data be available from the same specimens. The recent history of minke whale studies, in which clear taxonomic differences are being recognised in what was previously considered a single, highly variable species, suggest that similar studies on other balaenopterids will be equally useful, especially in establishing visual field characters.

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APPENDIX

CODING OF COLOUR CHARACTERS

1.Rostral saddle. The rostral saddle has not been documented in the Antarctic minke whale (Best, 1985; Bushuev & Ivashin, 1986). There is no indication of a rostral saddle in blue whales (True, 1904), humpback whales, gray whales, right or bowhead whales, nor the outgroup, *Physeter.* All are thus coded 0.

The rostral saddle was not documented in live *Caperea,* from South Africa (Ross et al., 1975). However, Arnold (1987) and Matsuoka et al. (1996, fig 1) show a pygmy right whale *Caperea marginata* in which the head was distinctly lighter than the nape region, and it is thus coded rostral saddle present (1)

The rostral saddle is coded as present (1) in sei whales based on the photographs in Clapham (1997: 52,55). The latter picture shows a dark eye stripe and light head (i.e. rostral saddle); this pattern was noted in 7% of sei whales examined in the Antarctic by Matthews (1938).

The rostral saddle is coded present (1) in the common minke whale based on its occurrence at least in North Pacific minke whales. The light head is obvious in Dorsey et al. (1990, fig. 7 (right sides of 7A, 7C, 7D, 7E, 7H; left side of 7E; Lien & Katona 1990: 33). The light head in more photographs of the right side may indicate that the rostral saddle is better developed on that side in north Pacific minke whales, as is the case with the dwarf minke whale. A surfacing Northern Hemisphere minke whale shows a distinct right posterior extension of the rostral saddle with a scalloped posterior margin (Hoelzel & Stern, 2000: 39), as is seen in dwarf minke whales.

Although it is the asymmetric nature of the colour pattern which has been emphasized in fin whales *Balaenoptera physalus* (e.g. underwater photographs in Kiefner, 2002: 66,67) it is clear that the whole head can be light coloured, as a rostral saddle (e.g. aerial photos in Leatherwood et al., 1988, fig 26; Reeves & Mitchell, 1991, fig 11). On the right side, it is defined by the dark eye stripe, which is perhaps all that is left of a more extensive dark nape field; the details of the left nape field are unclear. At least on the right side, the rostral saddle is very well developed, thus it is coded as 2. Similarly, based on data in this paper, the rostral saddle of the dwarf minke whale is coded well developed (2).

2. Blowhole streaks. There is no evidence for blowhole streaks in sperm, right, bowhead, pygmy right, gray, humpback or blue whales, despite the abundance of detailed photos of live animals. All are scored 0 (blowhole streaks absent).

Minasian et al. (1989: 49) have a photograph of a northwest Atlantic fin whale with what appears to be a very clear left blowhole streak; the right blowhole streak is more obscure and appears to run just medially to the posterior extension of the right rostral saddle. A fin whale from the Gulf of California (Readers Digest, 1997) shows what appears to be a distinct left blowhole streak although it is partially obscured by dappling of the water surface. Blowhole streaks are visible in underwater video of a fin whale in the BBC documentary *Blue Planet (Tidal seas* episode).

Blowhole streaks are not visible in underwater photographs of sei whales in Williamson (1972) but the whole dorsal surface of the whales was heavily dappled from surface light refraction. The photograph of a sei whale (Clapham, 1997: 52), shows what appear to be blowhole streaks in the same general position as in the dwarf minke and fin whales. Images of Bryde's whales from Western Australia feeding on bait balls (BBC documentary series *Wild Australasia: Southern seas)* show what appears to be blowhole streaks.

Blowhole streaks occur in at least some North Pacific minke whales (Norris & Prescott, 1961, pl. 40b; Hoelzel & Stern, 2000: 39). They appear similar to the blowhole streaks of dwarf minke whales, as documented in this paper. Turner (1891-92: 49), describing a minke whale from Scotland, noted that 'a thin grayish band passed for several inches horizontally behind the blowholes'- a good description of blowhole streaks.

Based on these literature records for finback, sei and common minke whales, and this paper for dwarf minke whales, all are scored as 1 (blowhole streaks present). Best (1985) first documented blowhole streaks, in the Antarctic minke whale. They seem to be better developed in that species than in the dwarf minke whale (Best, 1985) or in the northern hemisphere minke whales. The Antarctic minke whale is thus coded 2 (blowhole streaks well developed).

3. Dark nape field. Sperm, right, bowhead, gray and humpback whales have a uniform dorsal colouration and there is no clearly defined nape streak in photographs of any of those species. They are thus coded 0 (dark nape field absent).

The nape area appears dark, contrasting with a light rostral saddle in pygmy right (Matsuoka et al., 1996), fin (True, 1904; Kiefner, 2002) and sei whale (Clapham, 1997). There are varying degrees of light grey just above the flipper in fin whales, containing light streaks diverging forwards and posteriorly from the flipper (True, 1904). In fin and sei whales, the darkest area of the nape may be restricted on the right side to a dark band running dorsally and backwards from the eye. Nevertheless there is a dark nape area and pygmy right, fin and sei whales are all coded as 1 (dark nape field present).

The dark nape region is obvious in photographs of northern hemisphere minke whales (e.g. Norris & Prescott, 1961, pl. 39; Mitchell,1975, fig. 2 of Newfoundland specimen; Leatherwood et al., 1988, fig. 110), as well as Antarctic minke whales (Kasuya & Ichihara, 1965) and dwarf minke whales (this paper). All minke whales are therefore coded 1.

In blue whales from the northwest Atlantic, there is a generally lighter patch above and in front of the flipper in the nape region (True, 1904, pl. 48,2). It is coded 2 (nape field light).

4. Form of dorsal portion of nape streak. There is no evidence of a nape streak in sperm, right, bowhead, gray, humpback or blue whales. Even foetal blue whales appear to lack a nape streak (Mackintosh & Wheeler, 1929) in contrast to its development in foetal fin and sei whales (see below). All these species are coded 0 (nape streak absent).

A V-shaped chevron occurs in the nape region of at least some individuals of pygmy right whale (Arnold, 1987: 266-267, 268; Matsuoka et al., 1996, fig 1).). It also occurs in fin whales (e.g. True, 1904; Mackintosh & Wheeler, 1929; Aguilar et al., 1990), who described right and left chevrons although these may link dorsally as a V (Lien & Katona, 1990: 30)). It occurred in about 8% of Antarctic sei whales examined by Matthews (1938). This V-shaped chevron seems to be developed in foetal fin (Mackintosh & Wheeler, 1929) and sei (Matthews, 1938) whales. A thin V-shaped nape streak was visible on a Bryde's whale from Western Australia (*Wild Australasia: Southern seas*). It is also present in adult Antarctic minke whales (Best, 1985; Bushev & Ivashin, 1986); it may be extensive and with a dark centre, as has been described for the fin whale, but is less diffuse than in the common and dwarf minke whales (see below). Based on these literature records a V-shaped nape streak does appear to be present in pygmy right, fin, sei and Antarctic minke whales, which are therefore all scored 1.

The nape streak appears to be present in northern hemisphere minke whales although it is usually seen only on photographs of live animals or those freshly stranded. Hoelzel & Stern (2000: 39) gives a clear dorsal view, showing that the nape streak is a thin transverse light grey line as in the dwarf minke whale. It appears to be continuous across the back but is faint. Leatherwood et al. (1988, fig. 105) shows an individual photographed off San Diego in which the nape streak has a forward midline peak.

Photo-ID views of north Pacific minke whales clearly show side views of the nape streak, called the 'shoulder streak' by Dorsey et al. (1990). It can be a fine line (Dorsey et al., 1990, fig. 7B,D right side) or more diffuse (Dorsey et al., 1990, fig. 7E, right side), mirroring the variability in dwarf minke whales. It appears to insert near the axilla of the flipper (Martin, 1990: 79; Hoelzel & Stern, 2000: 34) rather than near to the leading edge of the flipper or anterior margin of the thorax patch as in dwarf minke whales.

Thus in the common (literature records above) and dwarf (this paper) minke whales the dorsal portion of the nape streak is a thin transverse line across the back which may be peaked forward on the midline (or more commonly, to left of midline) but which is more diffuse and variable in shape laterally and does not form a V. It is thus separately coded for those species as 2 (nape blaze linear to diffuse).

5. Ventral nape streak. In fin whales the backward V may merge with a posteriorly and dorsally directed light grey streak arising above or behind the flipper (True, 1904; Kiefner, 2002: 67). Together, these form a W-shaped pattern across the back and on the sides of the whale.

Best (1985) described the 'grey streak up side', a crescent shaped grey streak running up each side from above the flipper and meeting in the midline of the back. It was described as the 'W-shaped pattern' by Bushuev & Ivashin (1986, fig. 2: 6a-g), who figured variations in its dorsal contour. It appears to be analogous to the W-shaped pattern in fin whales.

It is not clear whether the W-shaped pattern is a discrete colour element or an amalgam of the dorsal V and a second, ventral colour element. We have treated it as a separate colour element and have coded it as present in the finback and Antarctic minke whales, in which it may rival the ear stripe as the most obvious colour element of the nape and shoulder region (e.g. Kasuya & Ichihara, 1965, figs 2,3). There is no evidence for the ventral nape streak in other mysticete species.

6. Ear stripe. There are no descriptions of ear stripes in sperm, right, bowhead, gray, humpback or blue whales nor are they evident in photographs of those species. Underwater photographs of a juvenile pygmy right whale (Martin, 1990: 61; Menkhorst, 1995: 308) shows a light grey triangle with its apex on the ear aperture and expanding ventrally to its maximum extent on the nape region in front of the flipper. It is unclear if this is more than an individual variation and it is not considered evidence of an ear stripe. Thus all the above species are coded 0 (ear stripe absent).

True (1904) noted that a constant and obvious feature in northwest Atlantic fin whales was a whitish line starting from the ear on the right side, curving first upwards and then downwards to insert on or near the flipper insertion. A similar white marking was noted by True on the left side, except that it usually started at the eye, ran through or under the ear and downwards to the flipper. An ear stripe is visible on the left side of an Antarctic finback whale (Mackintosh & Wheeler, 1929). What appears to be a small light ear stripe appears in a Bryde's whale from Queensland (Paterson & van Dyck, 1988, fig. 3); an ear stripe was also visible in a Bryde's whale from Western Australia (*Wild Australasia*). It has been described in Southern Hemisphere sei whales (Matthews, 1938) in which its form is said to resemble that in fin whales.

Omura & Sakiura (1956) noted ear stripes in North Pacific common minke whales. A light ear stripe appears in a Norwegian specimen (Clapham, 1997: 109) and a northeast Pacific minke whale (Nowak, 1999). The latter is apparently the same specimen as shown in Norris & Prescott (1961) but the glare on the shoulder region in their pl. 39 obscured any signs of an ear stripe.

Best (1985) did not comment on ear stripes in the Antarctic minke whale. It was shown by Kasuya & Ichihara (1965) as a light streak curving ventrally to meet the base of what we consider the nape streak, above the flipper. Bushuev & Ivashin (1986) noted that it was 'characteristic of most [Antarctic] minke whales' but described many variations in extent and colouration.

In our experience, an ear stripe is uncommon in dwarf minke whales but may be present. Thus this character is coded as present (1) for finback, sei, common, Antarctic and dwarf minke whales.

7. Basal flipper colouration. The flippers of sperm, right, bowhead, pygmy right, gray and humpback whales are uniformly coloured throughout. In humpback whales, there appears to be considerable geographic variation in the extent of dark grey on the upper surface of the flipper, even within a single aggregation of individuals (e.g. groups in Hawaiian waters in Chadwick & Nicklin, 1999: 112-113). The sei whale also appears to have a monotone coloured flipper. These species are thus coded as 0 (uniform).

In northwest Atlantic blue whales up to the distal one quarter of the flipper as well as all of the leading and trailing edges of the flipper may be a light, almost white colour (True, 1904). This prominent white leading edge may also be evident in southern hemisphere blue whales (Kiefner, 2002: 47). Northwest Atlantic finback whales described from a Newfoundland whaling station were said to have dark grey flippers but with a white leading edge (True, 1904, pl. 48,1). Up to the proximal one quarter could be 'abruptly and conspicuously lighter than the remainder'. A thin dark line could run across the flipper at the margin of the light and dark grey on the flipper (True, 1904). However, in living animals the flipper may be light grey throughout (e.g. Darling & Nicklin, 1988: 878-879). A generally light grey flipper with a white leading edge is evident on the left side of a fin whale (Kiefner, 2002: 67), though that individual appears to have some dark grey at the base. The blue and fin were thus coded as (1) generally uniform colouration but with white leading edge. A Bryde's whale from West Australia also showed a white leading edge to the flipper (*Wild Australasia*). Dwarf minke whales have a consistently white flipper base and are coded 2.

Common minke whales seem consistently to have a dark flipper base (e.g. Omura & Sakiura, 1956, pl. 2; Norris & Prescott, 1961, pls 39, 40; Mitchell & Kozicki, 1975, fig. 9 to cite just a few of the photographs available). Kato et al., (1992) described an obscure white band on the flippers in 18/63 minke whales from the Sea of Japan taken in April to June; their fig. 2, however, illustrated a dark base even in their type III flipper, with the obscure band. In the 2.7m female illustrated by Norris & Prescott (1961), there appears to be a tongue of dark pigment from the shoulder region onto the flipper base, rather than a discrete band; their plate 40 indicates that the entire leading edge of the flipper is white. We can not say whether this is a regular feature of newborn or very young animals or simply individual variation. It does not change the fact that the overwhelming number of common minke whales have a dark base and are thus coded (3)

In Antarctic minke whales, Best (1985) recognised a 'plain' monotone flipper with an "almost white" leading edge (type 1) and a 'two-tone' flipper with a darker grey base (type 2), which could be further classed as weakly (2a), moderately (2b) or strongly (2c) two tone. There was colour asymmetry, with the two tone flipper more common on the left side (14/17 cases) and with a more strongly two-tone pattern on the left side. In the strongly two-tone flippers, there appeared to be a dark flipper base as distinctly developed as in northern hemisphere minke whales. Given this colour asymmetry, two analyses were run, the first with the flipper base coded (1), corresponding to the montone flipper with light leading edge and then coded (3), indicating the occurrence of a dark flipper base on the left side of some individuals.

8. Distal flipper colouration. The flippers of sperm, right, bowhead, pygmy right, gray, humpback and sei whales were uniformly coloured and, as with the basal flipper colouration, were coded 0.

The distal portion of the fin, blue and Antarctic minke whales were uniform but with a light leading edge (Best, 1985; Bushuev & Ivashin, 1986) and coded 1. This colouration also is present in at least some Bryde's whales.

In all Northern Hemisphere minke whales, the distal tip of the flipper is dark grey (see references to photographs above). The photographs in Omura & Sakiura (1956) and Mitchell & Kozicki (1975) show particularly well (1) the most extensive development of white along the leading edge of the flipper and (2) the blurring of the margin by a band of lighter grey which extends into the white of the flipper to a variable extent as streaks. Mitchell & Kozicki (1975, fig. 9) showed that the trailing edge of the flipper is dark from the tip to the axilla. All these features are identical to the distal flipper pigment of dwarf minke whales, as documented in this paper. Thus the common and dwarf minke whales were coded as 2 (dark grey distal flipper colouration).

9. Axillary patch. There is no indication of an axillary patch in sperm, right, bowhead, gray, humpback or blue whales. A juvenile pygmy right whale from Victoria, Australia (Menkhorst, 1995: 308) appears to have a dark streak rising obliquely from the flipper axilla onto the flank areas but it is not clear that this is an axillary patch. All the above species are coded 0 (axillary patch absent).

True (1904) noted that in the fin whale the light basal area of the flipper 'may be defined posteriorly by a dark grey line running across the pectoral to the axilla and thence to the back'. This dark streak, originating from the axilla, was also illustrated in a diagram of colour variations in finback whales by Aguilar et al. (1990).

In common minke whales, there may be a dark pigmented area running backwards from the axilla. It may vary from a very thin line (Hoelzel & Stern, 2000: 34; Norris & Prescott, 1961, pl. 39)- between the thorax blaze and the shadow of the flipper) to a triangular patch with the apex at the axilla (Omura & Sakiura, 1956, pl. 2, upper; Leatherwood et al., 1988, fig. 110). It is shown as a distinct colour element in the painting by Foster (Leatherwood & Reeves, 1983: 66) which best agrees with the colour patterns shown in photographs of the north Pacific minke whale.

A similar dark patch, which may be triangular, also occurs in some Antarctic minke whales, running from the axilla to between the nape blaze and thorax patch (Bushuev & Ivashin, 1986, fig. 2:7a-c). Based on these literature records, an axillary patch is scored present (1) in fin, sei, common and Antarctic minke whales.

The axillary patch of dwarf minke whales occasionally may be reduced (and thus similar in extent to the pigment in common and Antarctic minke whales) but is generally strongly developed and was coded 'well developed' (2).

10. Thorax field. The colouration of sperm, right, bowhead, gray and blue whales is uniform; right whales may have patches of white ventrally (sometimes extensively) and bowhead whales have a white-tipped lower jaw but there is no indication of a light grey lateral field and the pattern overall is uniform.

The colouration of the pygmy right whale is not clear but based on descriptions and photographs, appears to be darker above with a consistently lighter belly. There seems to be a clear black and white transition in humpback whales, with white sometimes extending high on the sides below the dorsal fin (Lillie, 1915; Burton, 1991, fig. 3, who illustrated four variants with diagrams and photographs respectively). Although they may appear to be quite differently coloured, both pygmy right whale and humpback whale are coded 1- basically a two tone pigment with a darker back and lighter underside, with no indications of an intermediate light grey pigment field.

There seems to be at least some transitional light grey in fin whales (it is apparent in video sequences in the *Blue Planet* series) but the situation is less clear in sei and Bryde's whales. For the latter species, Baker (1983: 72) illustrates what appears to be a grey side although the image is somewhat overexposed; Leatherwood et al. (1988, fig. 40) illustrated a Bryde's whale with an apparent flank patch high on the sides in front of the dorsal fin. Bryde's whales filmed feeding in Western Australia also appeared to have a light grey transitional lateral field (BBC: *Wild Australasia*). The situation is clearer in the minke whales, with a light grey lateral field clearly visible in common, Antarctic and dwarf minke whale species. For the analysis, a light grey lateral field has been considered a general balaenopterid feature and this field has been coded as present (2) for both fin and sei whale.

In addition to the grey lateral pigment, however, all minke whales have a dark, cape-like thorax field. It is a consistent feature of dwarf minke whales (this paper). This dark, ventrally directed triangular field separates the thorax patch and flank patch and is evident in field photos of northern hemisphere minke whales (Dorsey et al., 1990, figs 6,7; Reeves & Mitchell, 1991, fig. 13). Parallel dark stripes (our 'tiger stripes') run from the thorax cape onto the thorax patch and flank patch (e.g. Dorsey et al., 1990, fig. 7A right and left, 7E right side), as in dwarf minke whales.

A similar cape-like field separates the thorax patch and flank patch in Antarctic minke whales, however rather than being a broad equilateral triangle, it seems to have an almost vertical posterior edge and extends further dorsally (Best, 1985; Bushuev & Ivashin, 1986, fig. 2:9a-e). Dark parallel stripes from the thorax field were recorded in a minority of Antarctic minke whales (1.7% of males, 4.5% of females) by Bushuev & Ivashin.

Given the consistent occurrence of a thorax field and flank patch in common, Antarctic and dwarf minke whales, they are coded (3).

11. Caudal chevron. There is no evidence of any caudal chevrons in sperm, right, bowhead, pygmy right, humpback, sei or blue whales. These are coded 0 (chevron absent). A single chevron is documented for Northern Hemisphere (True, 1904) and Southern Hemisphere (Mackintosh & Wheeler, 1929) fin whales, which are coded as 1.

Dwarf minke whales consistently have two caudal chevrons (this paper). Both common (Norris & Prescott, 1961, pl. 39; Leatherwood et al., 1988, fig. 110) and Antarctic minke whales (Best, 1985) also appear to consistently have two caudal chevrons. All the minke whales are thus coded 2 (for double chevron).

12. Peduncle streak. This feature has only been documented within minke whales; all other species are coded 0 (for absent).

In the Antarctic minke whale, the peduncle patch is restricted to the ventral field, where it is delimited by the caudal chevrons (coded as 1). In dwarf minke whales, the light colour continues as a light streak up the side of the peduncle (coded 2). This may also be the case in the common minke whale, based on a photograph of a 2.7m female minke whale from the North Pacific (Norris & Prescott, 1961, pl. 39). On the basis of that record, the peduncle streak is also coded as present (2) in common minke whales.

13. Asymmetry. Based on a review of the literature, asymmetry does not appear to be present in sperm, right, bowhead, pygmy right, gray, humpback or blue whales (although Sars (in Arvy, 1977) noted that in blue whales the right side of the face was lighter than the left). These species are recorded as 0 (asymmetry absent).

Subtle asymmetry was documented in about 10% of the sei whales examined by Matthews (1938). His account appears to be somewhat contradictory, with statements that the whole of the pigment is 'shifted slightly to the right' and with white on the ventral grooves somewhat more developed 'on the left side of the median line', but also that the asymmetry is 'as in the Fin whale'. Asymmetry was reported in at least some Bryde's whales off southern Africa (Best, 2001).

Kasuya & Ichihara (1965) noted that in the Antarctic minke whale that the darkly pigmented area of the jaw was broader on the left than the right side of the whales, that the white area on the upper lip was longer in the right and that the general head pigmentation was more extensive on the left. We have recorded instances of asymmetry in the mandible blaze, eye patch, extent of thorax patch, orientation of blowhole streaks, development of rostral saddle in the dwarf minke whale. In all cases, the right side is lighter. However, the impression is that pigment is shifted to the left: blowhole streaks (especially the left one) deviate to the left, where the dorsal nape streak is peaked forward, it is often canted to the left, the tip of the right thorax patch is oriented more towards the midline than in the left thorax patch, and the light grey clouds of pigment from the thorax patch may be oriented towards the left Similar subtle asymmetry is documented for common minke whales in the development of the rostral saddle (Dorsey et al., 1990; Hoelzel & Stern, 2000) and the blowhole streaks. Subtle asymmetry (1) is thus coded for the sei and all minke whale species.

The classic case of asymmetry is the fin whale, with a completely white lower right jaw and more extensive light grey on the right shoulder region. This asymmetry is well developed (acting as a field character for the species) and is coded 2. Similar asymmetry appears in *B. omurai*.

ADDITIONAL COLOUR ELEMENTS NOT INCLUDED IN THE ANALYSIS. *White flipper band in common minke whale.* A white band bounded by a dark base and dark flipper tip is characteristic of northern hemisphere common minke whales (see photograph references above). Although Kato et al. (1992) indicated that the white band was 'obscure' in some whales from the Sea of Japan, we know of no reports or illustrations of common minke whales with a monotone flipper, as in at least some Antarctic minke whales (Best, 1985) or with an ivory white base (as in all dwarf minke whales documented). Turner (1891-92), describing a specimen from Scotland, noted that the white portion of the flipper was 'partly interspersed with black patches'; this resembles the speckling in dwarf minke whale flippers. The flipper band is unique to the common minke whale and is thus of no phylogenetic significance.

Dark throat patch. Extensions of dark pigment from the nape field onto the throat region between the angle of the jaw and the insertion of the flipper can occur in north Pacific (Omura & Sakiura, 1956, pl. 1; Leatherwood et al., 1988, fig. 110) and North Atlantic (Mitchell & Kozicki, 1975, fig. 9) minke whales. Although considered evidence of a throat patch by Arnold et al. (1987), the extent of this ventral pigmentation seems to vary considerably in northern hemisphere minke whales. This contrasts with the consistent occurrence of a throat patch ('tongue of dark pigment extending onto the ventral grooves between the eye and the flipper insertion' of Best, 1985) in the dwarf minke whale (Best, 1985; this paper) and the consistent lack of such pigmentation in Antarctic minke whales (Best, 1985; Bushuev & Ivashin, 1986).

Although a generalised 'counter-illumination' pattern, with darker back and lighter belly is generally recognised in all balaenopterids except the blue whale, the extent to which dark pigments occurs on the underside is highly variable in humpback whales (e.g. Lillie, 1915), sei whales (Andrews, 1916; Matthews, 1938), fin whales (e.g. True, 1910; Mackintosh & Wheeler, 1929) and perhaps Northern Hemisphere minke whales. Although the contrast between the throat patch of dwarf minkes and the consistent lack of this feature in Antarctic minke whales seems clear enough, the throat patch can not be clearly related to ventral pigmentation in other rorquals and thus was not considered in the analysis.

Thorax patch. Dorsey et al. (1990, figs 6, 7) clearly document this feature in north Pacific common minke whales, calling it the 'thorax patch'; it was also described by Omura & Sakiura (1956). It is visible in a field photo of a North Atlantic common minke whale (Reeves & Mitchell, 1991, fig. 13). The thorax patch occurs above and behind the flipper and has a very sharply defined anterior margin, with a forwardly directly dorsal peak and a ventral extension almost to the axilla of the flipper (Mitchell, 1975, fig. 2; Leatherwood et al., 1988, fig. 110; Martin, 1990: 79; Hoelzel & Stern, 2000: 34). The dorsal margin is long and parallel to the line of the back, giving the appearance of a lightly coloured rectangle when seen in field photos.

Best (1985) described a 'thorax blaze' in Antarctic minke whales, as forming a roughly triangular lightly coloured extension running diagonally up from the axilla and then back again to about the same level. Although Best described this as part of the flank pigmentation, we separate the two elements, considering his 'thorax blaze' as analogous with the thorax patch.

Flank patch. The flank patch of northern hemisphere minke whales seems to run almost as far dorsally as does the thorax blaze. There are few photographs of this region other than on stranded animals which may have darkened in the sun. However there does appear to variable infilling of the flank patch by dark pigment (compare Dorsey et al., 1990, fig. 7C left side (extensive flank patch) and 7D right side (extensive infilling under the dorsal fin, with thorax blaze more extensive than flank patch). According to Best (1985), the flank patch in Antarctic minke whales extends higher on the sides than does the 'thorax blaze' (our 'thorax patch'). The extent of infilling has been undocumented.

Distinct thorax and flank patches appear to be restricted to minke whales and thus are of phylogenetic significance. However, the demarcation of these lateral light grey patches depends on the occurrence of the cape-like dark thorax field, which has been used in the analysis. Including the co-correlated thorax patch and flank patch as separate characters would unduly weight the analysis, so they were excluded.

White shoulder blaze. This colour element is unique to the dwarf minke whale and thus of no phylogenetic significance.